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Contribution No. 352

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DISCUSSION OF THIS PAPER IS INVITED. Discussion in writing (2 copies) may be sent to the Secretary, American Institute of Mining and Metallurgical Engineers, 29 West 39th Street, New York 18, N. Y. Unless special arrangement is made, discussion of this paper will close June 15, 1948. Any discussion offered thereafter should preferably be in the form of a new paper.

Wave Action on Structures

By Walter H. Munk*

(Tulsa and Los Angeles Meetings, October 1947)

Abstract

Generation of waves by storms, and the transformation of waves in shallow water by local bottom topography are briefly reviewed. A detailed description of water motion in waves explains the nature and distribution of wave forces. A numerical example dealing with forces and moments against vertical piles summarizes the principles involved.

Introduction

The oil industry is moving into the open waters of the Gulf of Mexico. The design and construction of offshore drilling rigs present a number of difficult problems, among them problems involving the action of waves on fixed and floating structures. This paper deals with our present knowledge of ocean waves as it pertains to these problems, and the principles involved in computing wave forces against fixed structures. It is hoped that the more difficult case pertaining to floating structures can be discussed at a later time. None of the engineering aspects of the problem are entered upon in this paper, yet an understanding of the principles presented here should be helpful in the solution of practical problems.

Nature of Wave Forces

Waves are capable of exerting almost unbelievable forces. During a gale, waves at the harbor entrance of Amsterdam Canal in Holland lifted a 20-ton concrete block, which was resting on the bottom in 12 ft of water, and deposited it on top of a pier which was 5 ft above the high water mark. At Wick Breakwater in Scotland, a mass of large stones in cement and bound together with iron rods, weighing 1350 tons, was broken loose and moved bodily! But one need not go to Holland or Scotland to find evidence of damage that waves are capable of inflicting (Fig 1 and 2).

What is the mechanism by which waves are capable of exerting such enormous forces? To answer this, we must consider briefly the nature of wave motion. When a wind blows over a wheat field, waves appear to travel across the field, whereas the wheat itself remains rooted, slowly swinging back and forth. Similarly, in the case of water waves, the wave *form* travels swiftly over the water surface, whereas the water particles oscillate back and forth, but scarcely advance. The speed of the wave form is called *wave velocity*, the speed of the water particles is called *orbital velocity*. This fundamental difference between wave velocity and orbital velocity was already recognized by Leonardo da Vinci. Orbital velocity is generally much slower than wave velocity except for a breaking wave, a case which is of particular importance in the application to engineering problems.

Forces exerted by the waves on obstacles are primarily due to the orbital motion. Since the orbital motion is oscillatory, moving once with the waves and then in the opposite direction, the forces themselves are oscillatory. However, at any given

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* Institute of Geophysics and Scripps Institution of Oceanography, University of California.

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instant the forces exerted will be the same, or nearly the same, as would be exerted on this obstacle if it were placed into a stream of uniform motion equal in speed to that of the orbital motion. An exception to this would occur if the resonance frequency of the entire structure would be close to the wave frequency, and the structure be set into violent vibrations.

FIG 1—HURRICANE-DRIVEN WAVE TOWERING MANY FEET IN THE AIR SMASHES AT THE APPROACH TO A BRIDGE JUST NORTH OF MIAMI BEACH, FLA., SEPTEMBER 19, 1947.
(Photograph by Acme Newspictures)

The dynamic pressure exerted by water moving uniformly past obstacles has been studied extensively, and the resulting law is well known in engineering practice:

$$P = \frac{C_D}{2}\frac{w}{g}V^2. \qquad [1]$$

P is the pressure in pounds per square foot; C_D the drag coefficient; w the weight in pounds of a cubic foot of water (65 lb for sea water); g the acceleration due to gravity in feet per square second; and V the velocity of water in feet per second past the obstacle. The ratio $w/g = 2$ approximately, and the equation can be written

$$P = C_D V^2. \qquad [2]$$

The drag coefficient C_D depends upon the shape of the obstacle and on Reynolds' number R where, with D designating the effective diameter,

$$R = \frac{VD}{\nu}. \qquad [3]$$

For water of about 70°F, the kinematic viscosity $\nu = 10^{-5}$ ft^2 per sec, so that R can be written $R = 10^5 VD$. For most structures subject to wave action the product VD will be considerably larger than 5 ft^2 per sec, and consequently $R > 5 \times 10^5$, indicating fully developed turbulent flow.

The values of Table 1 are selected from Table II of Rouse.[1]

The pressure exerted by waves on pier piles of |———| -section (assumed similar to rectangular plates) will be at least six times the pressure exerted on cylindrical pier piles of similar dimension! Expecting |———| -sections to withstand very large waves is somewhat like expecting a racing automobile housed in a model *T* chassis to establish a new speed record.

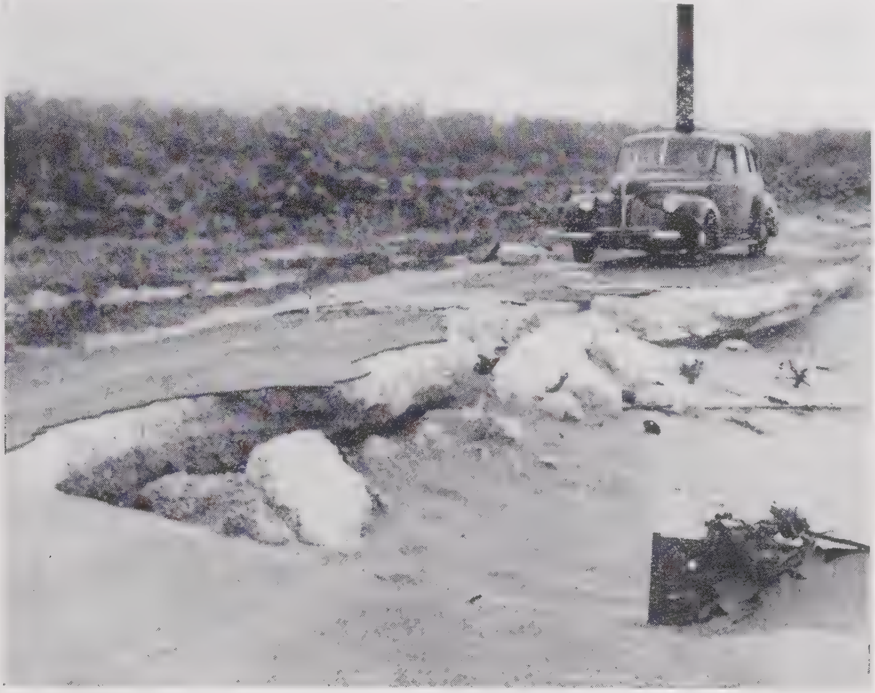

FIG 2—CLOSE-UP OF DAMAGE CAUSED BY WAVES SHOWN IN FIG 1. (Photograph by Acme Newspictures)

TABLE 1—*Approximate Values of the Drag Coefficient C_D*

Form of Body	R	C_D
Circular disc ⊥ to flow.........	$>10^3$	1.12
Long rectangular plate ⊥ to flow	$>10^3$	1.90
Long circular cylinder (axis ⊥ to flow).	$>10^5$	1.20
	$> 5 \times 10^5$	0.33
Sphere........	$>10^5$	0.50
	$> 3 \times 10^5$	0.20

Eq 2 can be checked by comparison with wave pressures measured by Gaillard[2] with dynamometers in Florida and Lake Superior (see Fig 16). Observed and computed values agree within 20 pct. This suggested to Gaillard that the sudden slaps of waves against structures, accompanied by loud noises and spray, are more spectacular than important, and that the truly destructive forces are due to the relatively sustained orbital motion of the water against obstacles. The pressures "apparently conform to the hydrodynamic laws governing action of a current flowing normally against a submerged plane" (Eq 1).

Although Gaillard's reasoning and measurements are fairly conclusive, it is essential to keep in mind other possible mechanisms by which waves are capable of

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[1] References are at the end of the paper.

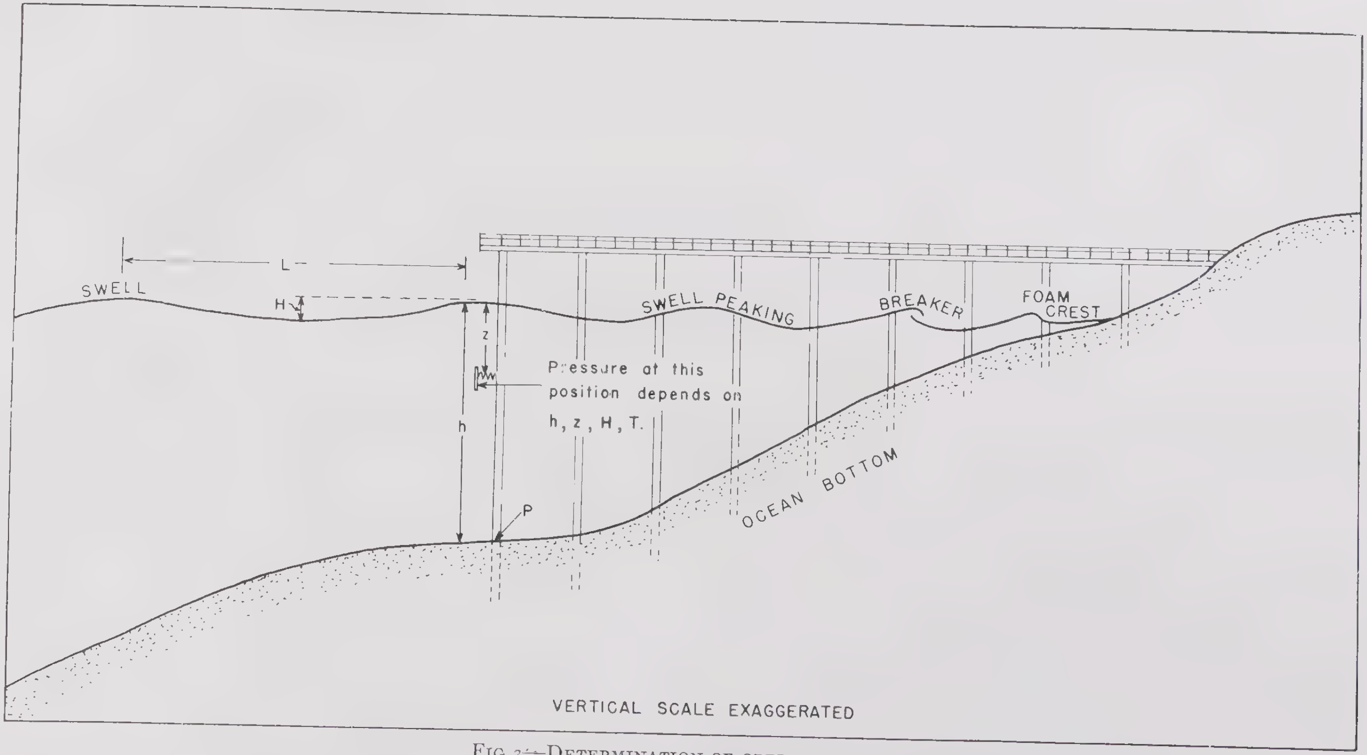
SWELL
L
H
z
h
P
Pressure at this position depends on h, z, H, T.
SWELL PEAKING
BREAKER
FOAM CREST
OCEAN BOTTOM
VERTICAL SCALE EXAGGERATED

Fig 3.—Determination of orbital velocity.

The wave height H denotes the vertical distance between trough and crest. The wave length L is the horizontal distance between two adjacent crests. The wave period T is the time interval between the arrival of successive crests at a fixed point. The pressure exerted by waves against obstacles depends upon the depth z of the obstacle; the total depth of water, h; the wave height, H; and the wave period, T. The figure gives a schematic presentation of changes in wave characteristics that occur as waves enter shallow water.

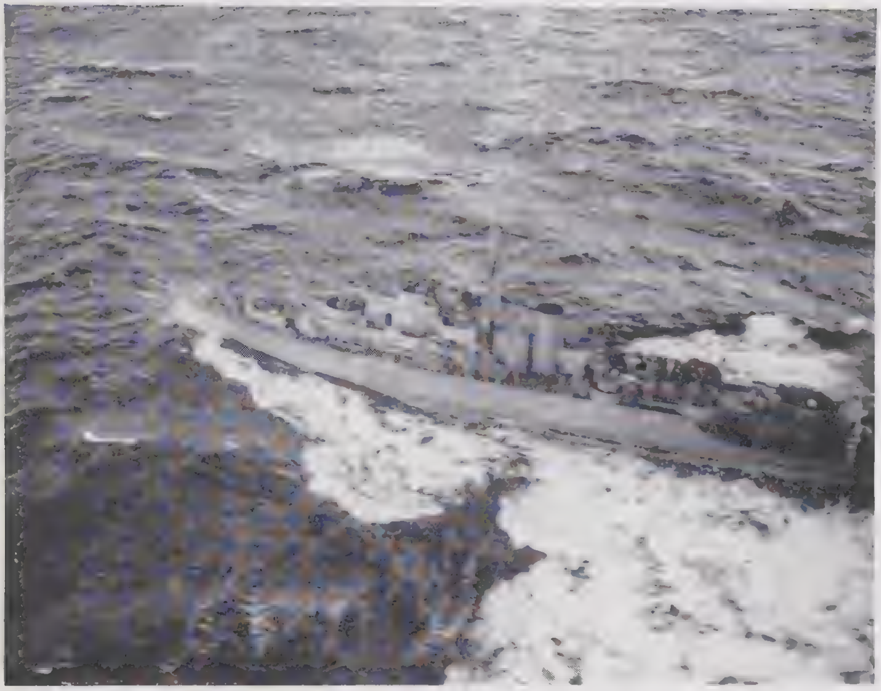

FIG 4—WAVES IN THE STORM AREA FORM AN IRREGULAR PATTERN KNOWN AS SEA.
(Official Photograph, U. S. Navy)

FIG 5—SWELL FROM A HURRICANE.
The farther the swell travels from the storm area where it was generated, the more regular it becomes.
(Official Photograph, U. S. Navy)

exerting forces, as these might not be negligible under special circumstances. Orbital motion past the obstacle will also exert frictional drag, and this might become important in the case of very rough surfaces, such as result when barnacles attach themselves to piling. This would also increase the effective diameter D. Another possible force, similar to the drag on ships associated with the formations of wakes, is related to wave formation by the obstruction. The role of resonance characteristics of the structure has already been mentioned. Finally, in the case of breaking waves, shock loads may be caused by the impact of water masses against structures. For very rigid structures, such as breakwaters, these may be large. For wooden piles or long beams there is probably sufficient "give" to avoid large impact forces.

Under ordinary circumstances the problem then is to determine the orbital velocities, vertical or horizontal, and to compute the wave pressures according to Eq 2. Unfortunately, the determination of these orbital velocities is not simple, as it involves four factors: the height H and period T of the waves (Fig 3), the distance z beneath the surface where the velocities are to be determined, and the total depth of the water, h. The wave height and period, in turn, depend upon the character and distance of the storm that formed the waves. To give a better understanding of the principles involved, we shall review briefly the origin of waves, the manner in which they are generated, changes that occur as they travel over the open ocean, and the transformation that takes place as the waves enter shallow water.

SEA—SWELL—SURF

If there were no wind, there would be no waves. Gusts of wind striking the water surface form waves which grow under the influence of the wind into a most irregular pattern known as *sea* (Fig 4). A heavy sea is raised when strong winds blow for many hours over large ocean areas. The height of the sea is determined therefore by three factors:[3]

Fetch—distance over which wind blows.

Wind speed—average speed of wind over fetch.

Wind duration—how long the wind blows.

Over land-locked areas, such as bays and small lakes, the fetch is limited by the size of the water body. In small bodies of water, very high waves cannot be formed Over large ocean areas the fetch depends upon the size of the storm system, but is often so long that the duration becomes a limiting factor.

Waves leaving the storm areas are known as *swell* (Fig 5). Their height gradually decreases, their length increases. After having traveled thousands of miles, they become a series of long, low, and fairly regular undulations known as ground swell. They may be all but hidden by short, irregular waves newly formed at the surface.

Each ocean region has its own characteristic swell conditions reflecting the general atmospheric circulation. Along the American West Coast the swell in winter is usually the result of storms traveling south of the Aleutians into the Gulf of Alaska. During the summer the American West Coast receives swell from the storms in the "roaring forties," several thousand miles to the south of the equator. Because of the prevailing westerly winds, our East Coast does not receive long regular swell, but high surf results from occasional local storms. For similar reasons, the Gulf Coast does not receive long, regular swell, but there, exceedingly high and dangerous waves are formed by hurricanes.

As waves enter shallow water a number of striking changes take place.[4] The wave velocity and length decrease, while the height usually increases, so that the wave gradually steepens (Fig 3). As the waves

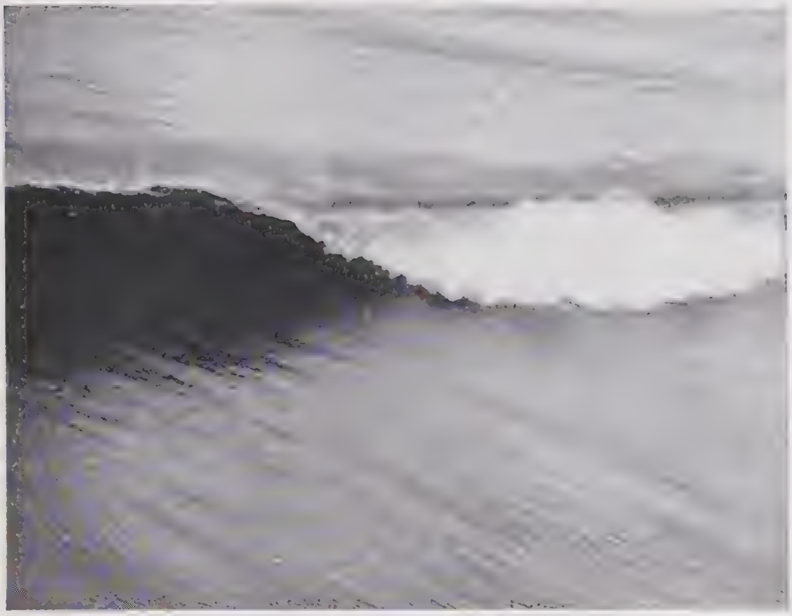

FIG 6—SURF CASED BY LONG REGULAR SWELL.
The crests curl and break with great intensity with all the energy going into the initial plunge.

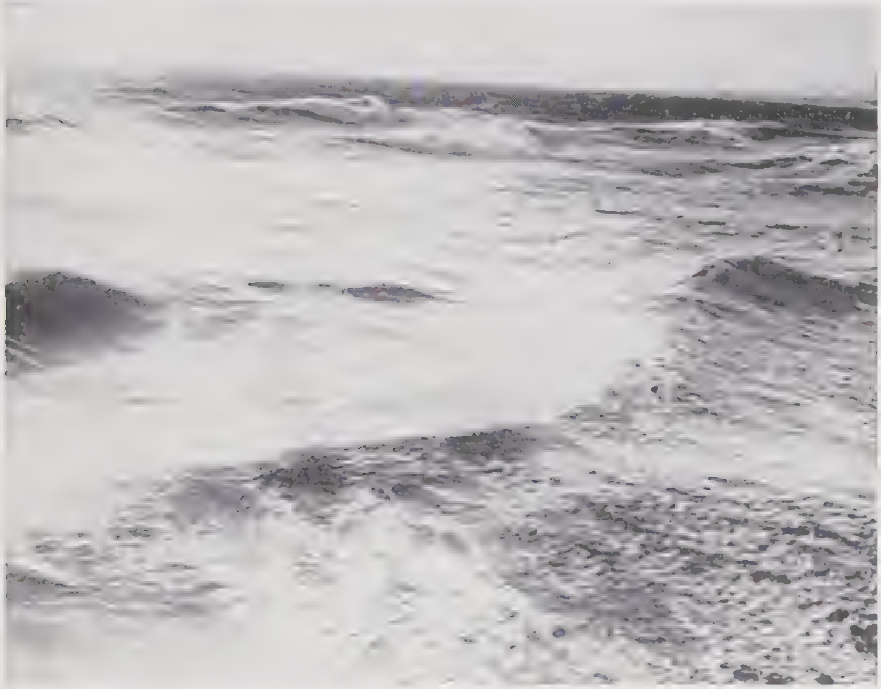

FIG 7—SURF CAUSED BY LOCAL STORM WAVES.
The top of the wave spills over gradually and breaking continues over a long time interval.

approach the surf zone, this process of steepening accelerates suddenly—the crests rise sharply from the water surface, become peaked, and break.

The changes just described are most noticeable for a swell from a distant storm (Fig 6). Waves formed by nearby storms, or by winds blowing directly toward the coast, have already considerable steepness out at sea, and whitecapping continues all the way to the surf zone. The top of the wave spills down the front, producing white foam and "boiling" on the leading slope, but with no real plunge of water (Fig 7). The last two figures typify two extreme types of surf: swell-surf and sea-surf.

Another important feature occurring in shallow water is the tendency of the crests to swing parallel to shore (Fig 8). This happens because the wave velocity decreases as the depth decreases, so that the portion of the crest nearer shore moves slowly while the portion of the crest in deeper water races ahead. The process is known as *wave refraction.*[5] Over a submarine canyon (Fig 9) the central portion of the crest is in deeper water and moves faster than the portion on either side. Consequently the waves fan out, resulting in divergence (low waves) over the head of the canyon and convergence (high waves) on either side. Piers and structures are often built opposite the heads of submarine canyons to take advantage of this feature (Fig 10). Underwater ridges near shore have an effect opposite to that of canyons (Fig 11). Waves passing over the ridge are in shallower water and are therefore retarded, and on

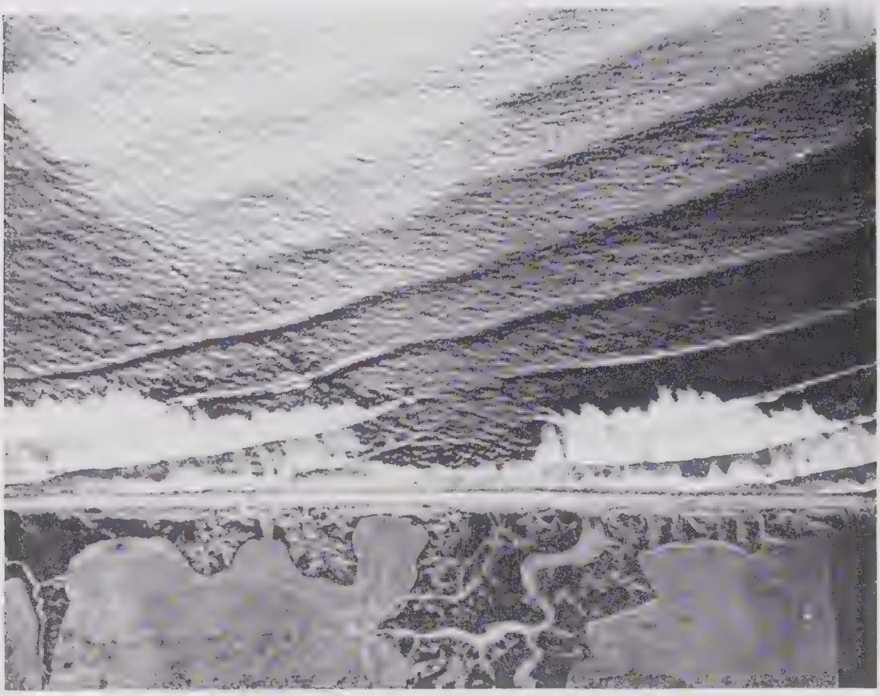

FIG 8—LONG WAVES FROM THE SOUTHERN HEMISPHERE APPROACH THE COAST NORTH OF OCEANSIDE, CALIF.

The upper portion of the wave crest is in deeper water than the lower portion and therefore travels with greater velocity. As a result, the waves tend to turn parallel to shore.
(Official Photograph, U. S. Navy)

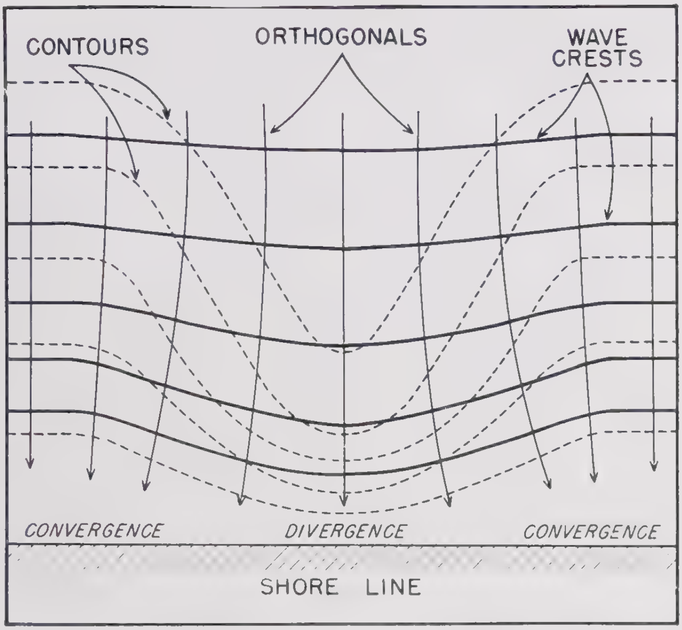
CONTOURS
ORTHOGONALS
WAVE CRESTS
CONVERGENCE
DIVERGENCE
CONVERGENCE
SHORE LINE

FIG 9—REFRACTION OF WAVES BY A SUBMARINE CANYON.
Waves move faster over the canyon than on either side of the canyon, resulting in divergence (low waves) over the mouth of the canyon and convergence (high waves) on either side.

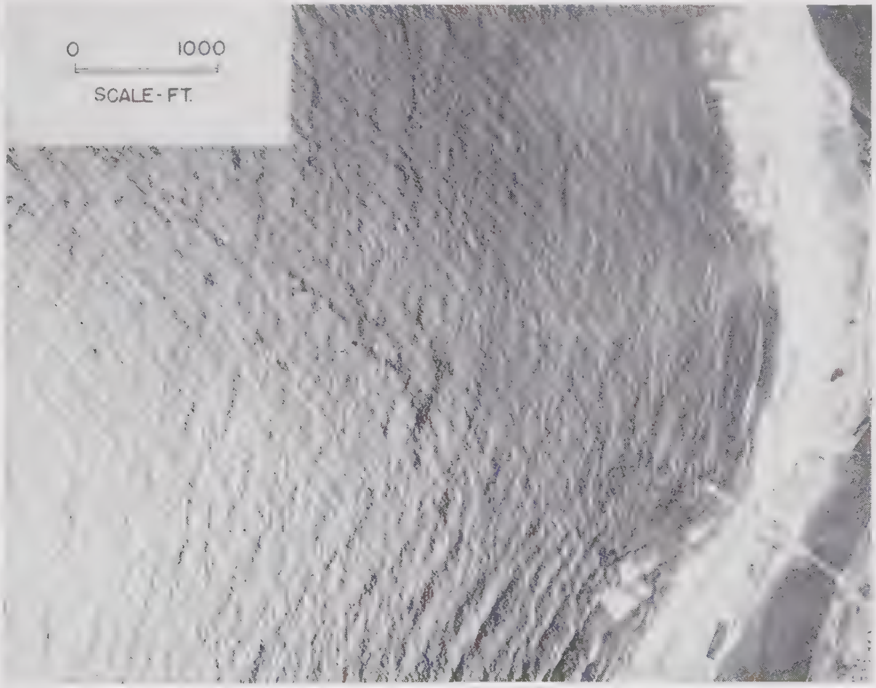
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FIG 10—WAVE REFRACTION AT MOSS LANDING.
Note the flat water at the end of the pier where the Monterey Canyon approaches the shore. (Photograph by Department of Engineering, University of California)

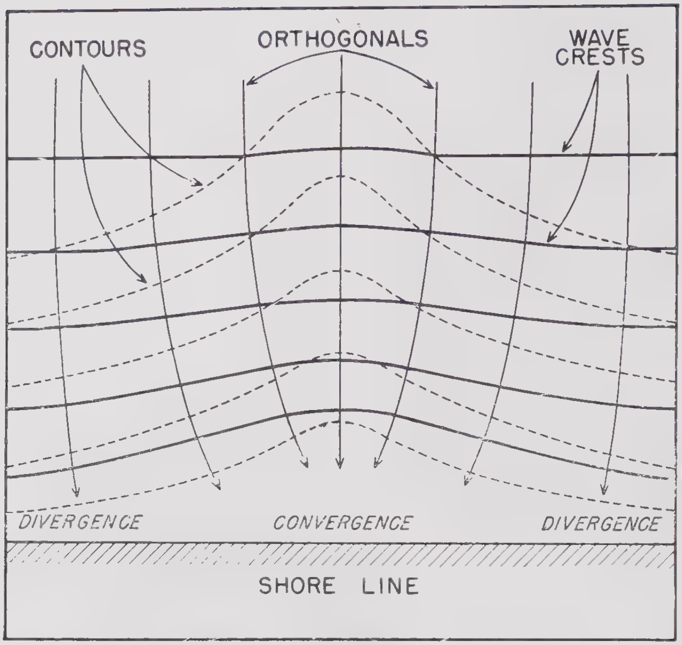
CONTOURS
ORTHOGONALS
WAVE CRESTS
DIVERGENCE
CONVERGENCE
DIVERGENCE
SHORE LINE

FIG 11—REFRACTION OF WAVES BY A SUBMARINE RIDGE.
Directly over the ridge waves lag behind, and on either side waves move ahead, creating a convergence (high waves) over the ridge.

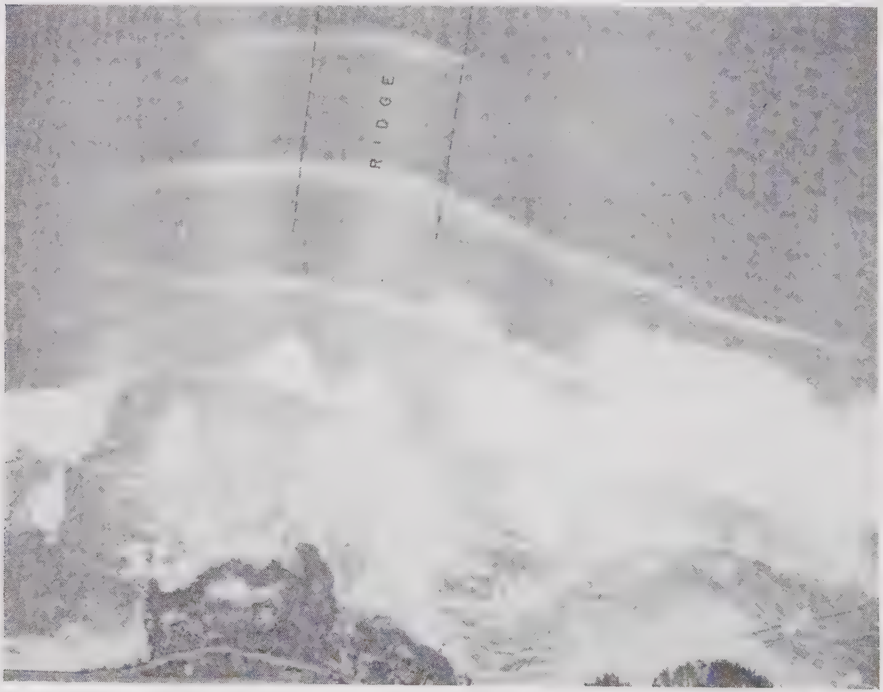

FIG 12—REFRACTION OF WAVES OVER RIDGE ALONG THE NORTHERN SHORE OF OAHU, T. H.
Over the ridge waves lag behind and are higher than on either side.
(Official photograph, United States Army)

either side waves move ahead creating a convergence over the ridge (Fig 12).

The selection of sites for the building of piers and other structures should be made with these factors in mind. *In some regions a slight change in location might mean a reduction of wave action by over* 50 *pct.*

COMPUTATION OF WAVE CHARACTERISTICS

In order to estimate wave action on structures it is first necessary to know the dimensions of the waves at the chosen locality. Depending upon the problem on hand one may be interested in the mean annual wave conditions, the mean seasonal wave conditions, the worst possible conditions, or conditions likely to be encountered for the next two days. For all but the last case it would seem reasonable to make use of past wave observations, but unfortunately very few observations are available which are adequate either with regard to quantity or quality. If we had to rely upon direct observations only, this discussion would be chiefly of academic interest.

In the preceding section the effects of storm conditions and bottom topography upon wave characteristics have been discussed. The relationships governing these effects have been determined, and it is possible to *forecast* waves with considerable accuracy, provided adequate weather maps and bottom charts are available. The method for forecasting waves was developed during the war in order to assist in the planning and operation of amphibious landings.[3,4,6,7,10] The method can be used in two ways: It can be used to forecast waves for a fixed time and day on the basis of current weather maps (usually it is not possible to make a reliable forecast for more than two days in advance); it can be used also to compute average and extreme wave conditions on the basis of historical weather maps, which are now available for the northern hemisphere for the past 18 years. In this manner statistical information regarding the distribution of wave heights and periods at a fixed locality and depth has been obtained without resorting to costly and prolonged observations.

ORBITAL MOTION

Returning to the discussion of orbital motion, it is necessary to give a precise definition of what is meant by deep and shallow water. Shallow water is water of depth (in feet) less than $2T^2$, where T is the wave period in seconds. In deep water, that is in water of depth exceeding $2T^2$, the bottom exerts no appreciable effect on the wave characteristics.

Fig 13 gives schematic representations of orbital motion of progressive waves in deep water, shallow water, and at the breaking point. The arrows in the upper left figure represent direction and speed of orbital motion in *deep water* at a given *instant.* Directly beneath the crest the water moves horizontally and with the wave; beneath the trough the water moves horizontally but in a direction opposite to that of the waves. Ahead of the crest the water is rising, behind the crest it is falling. The dashed curves represent streamlines, i.e., lines that are everywhere parallel to the direction of orbital motion.

The upper right figure shows the movements of *fixed water particles* during the passage of a wave, that is the particle trajectories, again in *deep water.* Each water particle describes a circle. To the extreme right of the figure, where the trough of the wave is located, the water particle occupies its lowest position. As the crest approaches, the particle moves clockwise and reaches its highest point at the instant the crest passes. After the crest has passed, the particle starts moving downward and reaches its lowest position with the arrival of the subsequent trough.

The two upper figures represent therefore the same phenomenon from two points of view. From either figure it can be seen that the maximum horizontal and vertical velocities are equal. The maximum horizontal and vertical loads, which are alternately exerted by the waves on a fixed beam with its axis vertical to the plane of the figure, must therefore also be equal. The maximum horizontal forces occur as the crest or trough passes, being directed with or against the direction of wave motion respectively; the maximum vertical forces occur midway between the passage of crest and trough, being directed upward ahead of the crest, downward behind the crest.

The orbital velocities are the largest at the surface and they decrease rapidly with depth. At a depth corresponding to $2T^2$ the velocities are negligible. This applies equally to the horizontal and vertical velocity components.

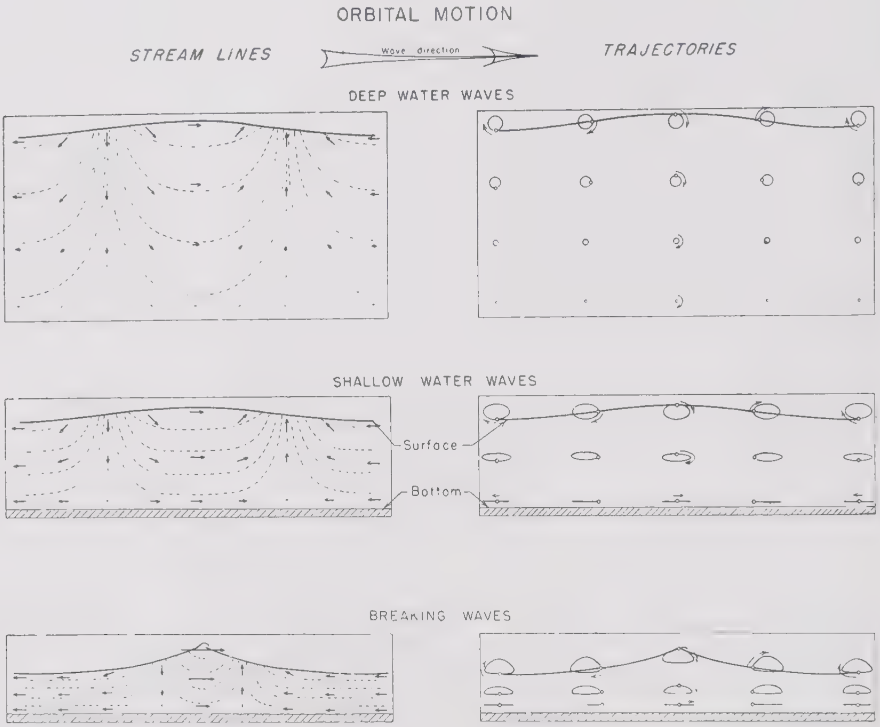

Fig 13—Orbital motion in progressive surface waves.

The dashed lines in the figures to the left are the streamlines, i.e., lines everywhere parallel to the flow. The direction and length of the arrows indicate direction and velocity of orbital motion. The figures to the right show the particle trajectories, i.e., the paths described by fixed particles of water. For further description, see text.

The central figures in Fig 13 show the streamlines and trajectories for wave motion in *shallow water.* Because of the restrictive effect of the sea bottom upon the water movements, the circular motion that existed in deep water is squeezed into elliptical motion and at the very bottom is distorted into linear back and forth movement. The motion is no longer symmetrical because the horizontal velocities exceed the vertical velocities. Otherwise, the orbital motion is similar to that in deep water, directed horizontally and with the waves directly under the crest, against the waves under the trough, upward or downward between crest and trough. The vertical movement ceases altogether at the bottom where the orbital motion consists entirely of back and forth movement of the water. A fixed beam in shallow water is subjected to larger horizontal forces than vertical forces. This is increasingly true the shallower the water and, for any fixed depth, the deeper the position of the beam beneath the water surface. The motion retains a certain degree of symmetry insofar as the maximum upward forces equal the maximum downward forces, and the maximum forces to the right equal the forces to the left.

For the case of breaking waves, as represented by the bottom two figures (Fig 13), even this symmetry does not hold. Practically all the forward motion is confined to the narrow region near the crest. Between crests we find long flat troughs during which the water moves relatively slowly opposite to the wave direction. To quote a numerical example, in the case of an 8-sec wave, the shoreward movement of the water will take place in 2 sec, the seaward movement in 6 sec. Directly at the crest of the breaking waves the water moves shoreward with the velocity equal to that of the wave itself. This feature may indeed be regarded as an explanation of why waves break. The orbital velocity beneath the crest decreases very rapidly downward, and equals only one-half the surface value at the level corresponding to the undisturbed sea surface, and one-third the surface value near the sea bottom. The vertical velocities are even smaller compared to the horizontal velocities than they were in the case of shallow water.

A fixed beam would therefore be subjected to the maximum possible pressure if it were located at the top of the breaking crest. But no matter where it is located, by far the largest forces will be directed horizontally, in the direction of wave motion, and will occur at the time when the wave is breaking over the beam. For most engineering problems a calculation of the maximum forces is probably sufficient.

THEORY

So far, the discussion of orbital motion has been purely qualitative. For deep and shallow water, all features which have been described are contained quantitatively in the equations:

$$u = U \cos\left(\frac{2\pi x}{L} - \frac{2\pi t}{T}\right), \qquad U = \frac{\pi H}{T}\,\frac{\cosh 2\pi(z+h)/L}{\sinh 2\pi h/L} \qquad [4a,\ b]$$

$$w = W \sin\left(\frac{2\pi x}{L} - \frac{2\pi t}{T}\right), \qquad W = \frac{\pi H}{T}\,\frac{\sinh 2\pi(z+h)/L}{\sinh 2\pi h/L} \qquad [5a,\ b]$$

which were derived theoretically by Airy in 1845. In these equations u and w are the horizontal and vertical components of the *instantaneous* orbital velocities, which change periodically with distance x and time t; U and W are the corresponding *maximum* values of orbital velocity expressed as functions of the wave height H; wave period T; wave length L; distance beneath the surface z; and depth of water h. The symbols *sinh* and *cosh* denote hyperbolic functions. These equations are complicated, but they can be presented in graphical form[8] and with some experience they are not difficult to handle. Objections have been raised against these equations because of assumptions and simplifications in their derivation. For that reason there has been a tendency to discount their practical use. Recently, especially during the war, the Airy wave equations have been checked in a large number of ways and found remarkably accurate (Fig 14). It may be said that for most practical problems the values obtained from Eq 4 and 5 are more accurate than could be determined by direct measurements with all but the most refined instruments. The usefulness of the Airy theory is born out by many successful applications; among them problems involving the forecasting of waves in shallow water, underwater depth determination, and the movement of submerged mines.

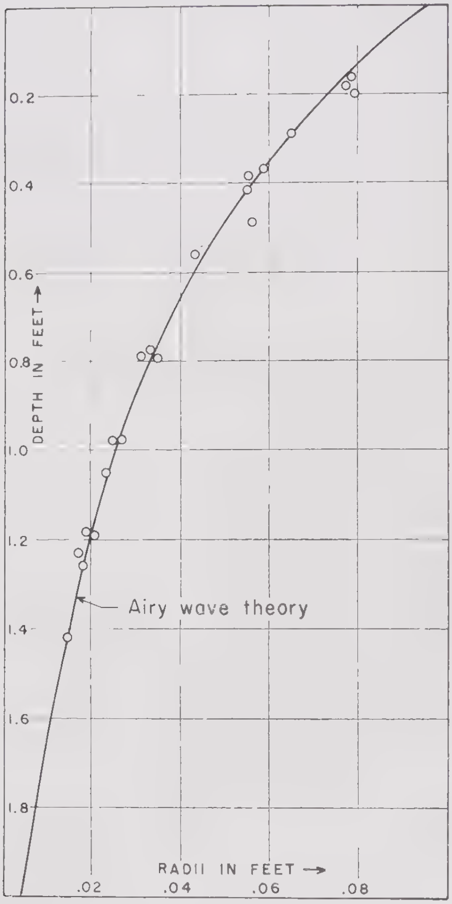

FIG 14—COMPARISON BETWEEN THEORETICAL AND OBSERVED VALUES OF ORBITAL RADII. (From Beach Erosion Board.[9])

The maximum horizontal pressures, P_h, are found by substituting Eq 4*b* into Eq 2:

$$P_h = C_D U^2. \qquad [6]$$

Similarly the vertical forces are given by the equation

$$P_v = C_D W^2 \qquad [7]$$

where the drag coefficient C_D now depends upon the shape and effective surface area of the obstacle relative to vertical flow. The net maximum forces at any instant are given by

$$P = C_D(U^2 + W^2) \qquad [8]$$

provided C_D is independent of the direction of flow.

The maximum horizontal forces from surface to bottom on a vertical beam or pile of constant diameter D are found by integration, using Eq 6 and 4*b*:

$$F = \int_{-h}^{0} P_h dz$$
$$= C_D D H^2 \frac{\pi L}{4T^2}(\coth\alpha + \alpha \sinh^{-2}\alpha), \qquad [9]$$

where $\alpha = 2\pi h/L$. The moments about the point where the pile is driven into the bottom (P in Fig 3) equal:

$$M = \int_{-h}^{0} P_h z dz = C_D D H^2 \frac{L}{16T^2}\cdot$$
$$(2\alpha \coth\alpha + \alpha^2 \sinh^{-2}\alpha - 1). \qquad [10]$$

But according to Airy's theory[10]

$$L = \frac{gT^2}{2\pi}\tanh\alpha \qquad [11]$$

which, when substituted into Eq 9 and 10 gives:

$$F = C_D D H^2 K_F,$$
$$K_F = \frac{g}{8}\left[1 + \frac{2\alpha}{\sinh 2\alpha}\right], \qquad [12]$$

$$M = C_D D H^2 h K_M,$$
$$K_M = \frac{g}{8}\left[1 + \frac{\alpha}{\sinh 2\alpha} - \frac{\tanh\alpha}{2\alpha}\right] \qquad [13]$$

The functions K_F and K_M, which are plotted in Fig 15 as a function of h/T^2, vary between relatively narrow limits, and may be considered nearly constant. The forces and moments vary approximately as the square of the wave height. The forces depend only slightly upon the depth of water, whereas the moments are roughly proportional to the depth.

Much less is known about breaking waves, with regard to both theory and observation. Some success has been achieved by the application of the so-called "solitary wave theory." According to this, the equations for forces and moments are more complicated than those derived from the Airy wave theory. It is hoped that they can be discussed at a later time, after the theory has been compared to observations.

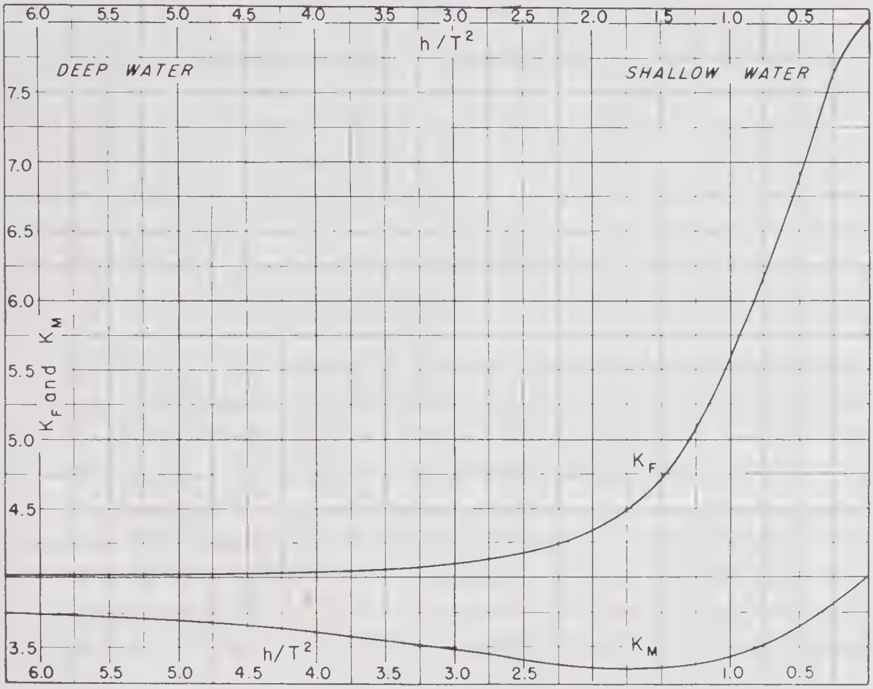

FIG 15—CORRECTION FACTORS FOR THE COMPUTATION OF HORIZONTAL FORCES AND MOMENTS AGAINST PIER PILES.
For description, see text.

For the special case of the forces exerted at the very crests of breaking waves, the orbital velocity equals the wave velocity, and is given by the equation

$$V_b^2 = g(h_b + H_b) \qquad [14]$$

where h_b is the depth of water at the breaking point, H_b the height of the breaking waves. Taking

$$h_b/H_b = 1.28 \quad \text{and} \quad h_b/H_b = 1.72 \qquad [15a, b]$$

for swell-surf and sea-surf respectively, and substituting these ratios into Eq 2 and 11, the result is

$$P_b = 73 C_D H_b \quad \text{and} \quad P_b = 87 C_D H_b \qquad [16a, b]$$

for the two extreme cases of long swell and short storm waves.

These formulas can be checked by means of measurements by Gaillard[2] with a dynamometer ($C_D = 1.31$). Observations at St. Augustine, Fla., refer to swell-surf and agree remarkably well with Eq 16*a* (see Fig 16). Observations at Lake Superior refer to sea-surf and agree on the average with Eq 16*b*. Eq 16*a*, *b* permit a rapid estimate of the dynamic pressure exerted at the tops of breaking waves. These dynamic pressures represent the worst possible pressures to which structures may be subjected by wave action.

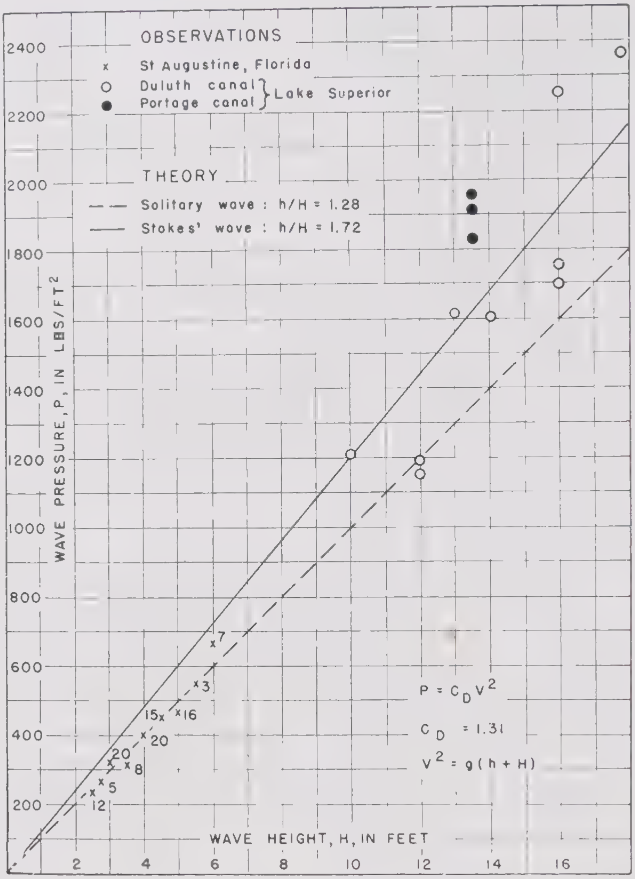

Fig 16—Comparison between theoretical and observed values of the pressure exerted at the crest of breaking waves.

Example

The principles discussed so far can best be summarized by an actual example. Suppose it is desired to find the maximum forces and moments exerted by wave action against vertical cylindrical piles of 3-ft diam, located off the Scripps Institution, La Jolla, Calif. Applying the methods of wave computation,[7] using Northern Hemisphere weather maps for the years 1936, 1937 and 1938, it was found that the maximum waves were 20 ft high in deep water, had periods of 9 sec, and approached from the west-northwest. The surf had the characteristics of swell-surf (Fig 6).

The wave characteristics were computed for selected depths, starting at a depth of $2T^2 \approx 160$ ft where they enter shallow water. The second line in Table 2 gives the height of these waves at various depths, taking also into account the effect of refraction.[10] The asterisks in the last two columns mean that the waves have broken, and that calculations are based on the solitary wave theory.

The third line in Table 2 gives the elevation of the highest point of the crest above the mean water surface. Prior to breaking, the highest point is one-half of the total wave height above the mean water level. At and after breaking the highest crest point lies ¾ of the wave height above the mean water level.

The Table next gives the values of maximum horizontal orbital velocities, U, which occur at the instant the wave crest passes the pile. These were computed according to Eq 4*b* and the solitary wave theory. The velocities decrease from the surface downward. They are by far the largest at the initial point of breaking, that is, at a depth of 20 ft.

The next section of Table 2 gives the wave pressures against the pier piles at various distances beneath the water surface, computed according to Eq 6 and using $C_D = 0.33$ (see Table 1). It is of interest to compare these with the pressure that a 100-knot wind would exert on the same piles. Taking the kinematic viscosity of air as 1.5×10^{-4}, one obtains the Reynolds' number 1.1×10^6, hence $C_D = 0.33$. The pressure is roughly 10 lb per sq ft, compared to a maximum wave pressure of 363 lb per sq ft! Yet according to a "practical" engineering rule, wave loads equal wind loads plus 30 pct!

The last two lines in Table 2 give maximum forces, respectively moments, according to Eq 12 and 13.

TABLE 2—*Calculation of Wave Characteristics, Forces and Moments against Vertical Piles off Scripps Institution Pier*

(Diameter of Piles: $D = 3$ ft
$C_D = 0.33$)

(Deep water wave height: 20 ft
wave period: 9 sec)

Depth of water, ft			160	100	40	20	10
Wave height, ft			20	14	12	15*	8*
Crest elevation above M.S.L			10	7	6	12	6
Maximum Horizontal Orbital Velocities, ft per sec.	Depth beneath M.S.L., ft	At crest	7	6	6	33	24
		0	7	5	5	14	10
		10	6	5	5	12	8
		20	5	4	4	11	
		40	4	3	4		
		100	2	2			
		160	1				
Dynamic Pressure against Pile, lb per sq ft.	Depth beneath M.S.L., ft	At crest	16	12	12	363	192
		0	16	8	8	65	33
		10	12	8	8	48	21
		20	8	5	5	40	
		40	5	3	5		
		100	1.3	1.3			
		160	0.3				
Total horizontal forces against pile, lb			1,740	1,000	1,000	9,300	2,400
Total moments against pile, lb-ft			214,000	66,000	21,000	216,000	27,000

* Waves have broken and solitary wave theory applies.

The stated depth refers to the time average of the depth at a given locality. In a heavy storm when the water is piled against shore, the average depth of water at a given locality would be larger than the average depth at the same locality before the storm. This rise in the mean water level (storm tide) may be of the order of 10 ft in very shallow water (0 to 20 ft), of the order of 5 ft in water of intermediate depth (30 to 40 ft), and negligible in deeper water.

SUMMARY AND CONCLUSIONS

The forces exerted by waves against structures are the result of a long chain of events, starting with the formation of a storm over the ocean, and followed by the generation of waves in the storm area (sea), the travel of these waves from the storm area (swell), and the transformation of the waves upon entering shallow water until they break (surf). Because of the active interest in meteorology many more data are available concerning the nature of the storms, than concerning any of the subsequent events.

Since the relationships between the various links of this chain are fairly well established, it is possible to forecast wave conditions from synoptic weather maps, or to compute past wave conditions from historical weather maps. In this manner one can obtain rational estimates of the wave conditions at a given locality.

From a knowledge of the wave height and period one can compute the water (orbital) motion, and then apply a well-known engineering formula to obtain dynamic pressures. The calculation is based on a hundred-year old theory which has received too little attention in engineering praxis.

Although there exists an urgent need for obtaining additional data on wave forces, either by measurements in the field or by model studies, the theory can serve a useful purpose as a guide in such measurements, and as a means of making preliminary estimates of the forces and moments to be expected.

ACKNOWLEDGMENT

It is a pleasure to acknowledge my indebtedness to Mercer H. Parks of the Humble Oil Company for having aroused my interest in the problems discussed here, and for having examined this paper.

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Contribution No. 353

Reprint from SEARS FOUND. JOURN. MAR. RES.

ERRATA

Journal of Marine Research

(Volume VII, Number 2)

Page 77, footnote 2 should read:

[2] Terms of the form $\frac{\bar{\tau}_x(y) - \tau_x(x_1y)}{\Delta x} \cdot \frac{dx_1}{dy}$, thereby neglected, are of small conse-

Page 78, line 1 should read:

by x_2; $\Delta P = P(x_1y) - P(x_2y)$ is the difference of P for two stations at

Page 82, Table I, last line should read:

8..........17.2-20.7..........1895........ 10.80.........10.85

Page 92, Equation (22) should read:

$$\frac{\partial P}{\partial y} = \frac{\Delta P}{\Delta y} - \frac{\partial P}{\partial x} \frac{1}{\tan \beta}, \tag{22}$$

Page 93, Equation (25) should read:

$$\begin{aligned} &+ \frac{bnK}{(k^2 - K^2)} \Big[k \cos 2k(\varphi - \varphi_0) \cos 2K(\varphi - \varphi_0'') \\ &+ K \sin 2k(\varphi - \varphi_0) \sin 2K(\varphi - \varphi_0'') \Big], \end{aligned} \tag{25}$$

Page 97, line preceding Equation (29) should read:

(1a) and (6):

THE EQUATORIAL CURRENTS OF THE EASTERN PACIFIC AS MAINTAINED BY THE STRESS OF THE WIND[1]

By

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INTRODUCTION

Sverdrup (1947) has shown that the main features of the distribution of mass in the eastern equatorial Pacific can be derived exclusively from the average wind stress distribution. In this paper the method for computing the wind stress will be developed, the treatment of the oceanographic observations will be discussed, the field of mass and of mass transport as derived from the oceanographic and wind observations will be dealt with, and finally an analytic solution will be given.

Counter currents have long been recognized from ships' records in each of the equatorial oceans, and their detailed structures in the Atlantic and Pacific Oceans have been described by Sverdrup (1932) and Defant (1936).

Montgomery (1940) and Montgomery and Palmén (1940) regarded the counter current as a downslope flow in the region of the calm belt, retarded only by frictional forces at the lateral and underlying boundaries of the current. They assumed that the hydrostatic head necessary to balance the friction was maintained by a piling up of water in the west due to the traction of the adjacent trade winds.

Stockmann (1945) has shown that it is necessary only that a sufficient lateral variation exist in the velocity of a wind of constant direction, blowing over a *closed homogeneous sea*, in order to give rise to a steady surface "compensation current," directed opposite to the prevailing wind. He has extended this theory to include the equatorial counter current developed in a *homogeneous ocean* (1946a, 1946b). In subsequent papers he includes *non homogeneous* conditions

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 353. This work represents results of research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the Navy Department under contract with the University of California.

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(1946c), and takes lateral friction into account (1946c, 1946d), as suggested earlier by Rossby (1936a) and Montgomery (1940). In all his papers, Stockmann has neglected the fact that the Coriolis parameter varies with latitude.

Sverdrup (1947) takes into account the variation with latitude of the Coriolis parameter in his treatment of wind-driven currents in a *baroclinic* ocean, but he neglects lateral friction. His theoretical treatment, as well as that of Stockmann (1946c, d), assumes that it is possible to explain the predominant characteristics of the permanent equatorial currents and accompanying distribution of mass in a nonhomogeneous sea by considering the wind stress as the only external factor explicitly involved. This would imply that the thermodynamics of the system can be ignored, and that only conservation of mass and of momentum need be considered. Such considerations evidently cannot completely account for the dynamics of the equatorial oceanic circulation, but it is intended here to show that a good approximation is achieved.

BASIC THEORY

Since we are dealing with a baroclinic medium wherein the pressure gradient generally vanishes at a moderate depth, it is apparent that horizontal motion and consequently frictional forces become negligible with depth. The net volume forces of the upper layer must therefore be balanced by the frictional stress exerted on the surface by the wind. The energy transferred to the water by the wind stress must be partly utilized by the work of cross isobaric flow and partly dissipated by turbulence in the upper layers if permanent currents are to be maintained.

Solutions in Terms of the Wind Stress. The principal assumptions, upon which Sverdrup (1947) bases his theoretical expressions, are as follows:

(a) there exists no acceleration,
(b) the fluid is free of lateral friction,
(c) the field of mass is in steady state,
(d) there exists a depth common to the whole fluid region at which horizontal and vertical motion is vanishingly small,
(e) vertical motion is absent at the surface, and
(f) the north–south component of wind stress is independent of longitude.

The above conditions lead to particular solutions of the equations of motion and continuity. The field of mass, which can be described in the horizontal by a function P, is given by the expressions

$$\frac{\partial P}{\partial x} = - R \tan\varphi \frac{\partial \tau_x}{\partial y} + \tau_x\,, \tag{1a}$$

and
$$\frac{\partial P}{\partial y} = - (x_1 - x_0) \tan\varphi \left(\frac{\partial \bar{\tau}_x'}{\partial y} \tan\varphi + R \frac{\partial^2 \bar{\tau}_x'}{\partial y^2} \right) - 2\omega \sin\varphi\, M_{x0} + \tau_y\,. \tag{1b}$$

The function $P = P\,(xy)$ is the vertical integral of pressure defined sufficiently by

$$P \equiv \int_0^d p\,dz + \text{constant}\,, \tag{2}$$

where $p = p\,(xyz)$ is the pressure, z is the vertical coordinate measured downward from the surface, and d is the depth of no motion. In (1) x and y are the east and north coordinates, respectively, of a rectilinear system whose origin is situated on the equator; $x_0 = x_0\,(y)$ is the position of the eastern boundary; and $x_1 = x_1\,(y)$ is the locus of an arbitrary path west of $x_0\,(y)$. The term R is the radius of the earth, φ is the latitude (positive north of the equator), $\tau_x = \tau_x\,(xy)$ and $\tau_y = \tau_y\,(xy)$ are the east and north components of wind stress, respectively, and $\bar{\tau}_x' = \bar{\tau}_x'\,(y)$ is the average stress between the continent and the western path, x_1, i. e.,

$$\bar{\tau}_x' \equiv \frac{1}{(x_1 - x_0)} \int_{x_0(y)}^{x_1(y)} \tau_x dx\,. \tag{3}$$

In (1b) ω is the angular speed of the earth, and $M_{x0} = M_x\,(x_0y)$ represents the eastward transport at the boundary.

The mass transport components are given by the expressions

$$M_x = \frac{x_1 - x_0}{2\omega \cos\varphi} \left(\frac{\partial \bar{\tau}_x'}{\partial y} \tan\varphi + \frac{\partial^2 \bar{\tau}_x'}{\partial y^2} R \right) + M_{x_0}\,, \tag{4a}$$

and
$$M_y = - \frac{R}{2\omega \cos\varphi} \frac{\partial \tau_x}{\partial y}\,, \tag{4b}$$

where $M_x = M_x\,(xy)$ and $M_y = M_y\,(xy)$ are the east and north components of the net mass transport of water per unit time through a column of depth d and unit widths. In terms of the density, $\rho\,(xyz)$, and the velocity components, $v_x\,(xyz)$ and $v_y\,(xyz)$, the mass transport is given by the expressions

$$M_x \equiv \int_0^d \rho v_x\,dz\,, \quad M_y \equiv \int_0^d \rho v_y\,dz\,.$$

Sverdrup approximates the American west coast by a north-south vertical boundary, in which case M_{x0} vanishes as required by the kinematic boundary condition (i. e., that the normal velocity at the boundary be zero). In general it can be shown, on the basis of (4b), that the transport for any vertical boundary takes the form

$$M_{x_0} = -\frac{R}{2\omega\cos\varphi}\left(\frac{\partial\tau_x}{\partial y}\right)_0 \tan\theta\,, \tag{5}$$

where the zero subscript refers to the boundary, and $\theta = \theta\,(y)$ is the bearing of the coast.

It can be demonstrated, however, that for the stress distribution of the *trade wind area,*

$$\left(\frac{\partial\tau_x}{\partial y}\right)_0, \quad \frac{\partial\bar{\tau}_x{}'}{\partial y} << \frac{\partial^2\bar{\tau}_x{}'}{\partial y^2}\,R.$$

Furthermore, the mean value of tan θ is approximately unity. This means that M_{x0} is negligible compared with M_x if $(x_1 - x_0)$ is of the same order of magnitude as R, and since tan φ is less than unity, (1b) reduces approximately to

$$\frac{\partial P}{\partial y} = -\,(x_1 - x_0)\,R\,\frac{\partial^2\bar{\tau}'_x}{\partial y^2}\tan\varphi + \tau_y \equiv f_2(\tau),\ \text{for } |x_1 - x_0| \geqslant R\,. \tag{6}$$

Likewise, (4a) becomes approximately

$$M_x = \frac{(x_1 - x_0)}{2\omega\cos\varphi}\,R\,\frac{\partial^2\bar{\tau}_x{}'}{\partial y^2} \equiv f_3(\tau),\ \text{for } |x_1 - x_0| \geqslant R\,. \tag{7}$$

Near the boundary the more exact equations, (1b) and (4a), must be used.

Equations (1a) and (4b) are averaged over the range from $x_1\,(y)$ to a second arbitrary path, $x_2\,(y)$, neglecting the boundary contributions to the derivative of mean stress[2]:

$$\frac{\Delta P}{\Delta x} = -\,R\tan\varphi\,\frac{\partial\bar{\tau}_x}{\partial y} + \bar{\tau}_x \equiv f_1(\tau)\,, \tag{8}$$

and

$$\bar{M}_y = -\frac{R}{2\omega\cos\varphi}\,\frac{\partial\bar{\tau}_x}{\partial y} \equiv f_4(\tau)\,. \tag{9}$$

In (8) and (9) $\bar{\tau}_x = \bar{\tau}_x\,(y)$ is the mean stress between the arbitrary boundaries, defined by an expression similar to (3), where x_0 is replaced by x_2; $P = P(x_1y) - P(x_2y)$ is the difference of P for two stations at the same latitude; and $\Delta x = (x_1 - x_2)$ is the range. In (9) $\bar{M}_y = \bar{M}_y(y)$ is the mean north-south transport between x_1 and x_2.

---

[2] Terms of the form $\dfrac{\bar{\tau}_x(y) - \tau_x(x_1y)\tau}{\Delta x}\cdot\dfrac{dx_1}{dy}$, thereby neglected, are of small consequence except for extreme variation of $\tau(xy)$ with x, or extreme values of dx_1/dy or dx_2/dy.

The approximations (6), (7), (8), (9) are dependent upon the existence of but one solid boundary. Consequently, a second kinematic boundary condition to the west cannot in general be satisfied by the solutions, and application to only a limited region of the Pacific is in order. This inadequacy of the solutions is presumably due to neglect of field accelerations.

Solutions Based Mainly on Oceanographic Data. The pressure can be determined to a very close degree of approximation by the hydrostatic equation,

$$dp = \rho dD, \tag{10}$$

where $D = D\,(xyz)$ is the geopotential depth. Since we are ultimately concerned with differences of P, the anomaly of geopotential between the isobaric surfaces $p(xyz)$ and $p(xyd)$ can be substituted for D. Integrating (10) and making use of (2), the function P takes the form

$$P = \bar{\rho} \int_0^d (\Delta D_d - \Delta D) dz + \text{constant}, \tag{11}$$

where $\Delta D = \Delta D(xyz)$ is the geopotential anomaly between the surfaces $p(xy0)$ and $p(xyz)$, and ΔD_d is that between the surfaces $p(xy0)$ and $p(xyd)$. The term $\bar{\rho}$ is the mean density of the column of depth d.

The mass transport can be obtained from the following expressions:

$$M_x = \frac{1}{2\omega \sin \varphi} \left(\tau_y - \frac{\partial P}{\partial y} \right), \tag{12a}$$

and

$$\bar{M}_y = \frac{-1}{2\omega \sin \varphi} \left(\bar{\tau}_x - \frac{\Delta P}{\Delta x} \right), \tag{12b}$$

obtained directly from the integrated equations of motion. These equations are a good approximation for $|\varphi| > 0$. To avoid an indeterminate expression at $\varphi = 0$, equation (12a) is differentiated with respect to y and solved for M_x at $\varphi = 0$. This yields

$$M_x = \frac{R}{2\omega} \frac{\partial}{\partial y} \left[\tau_y - \frac{\partial P}{\partial y} \right], \quad \varphi = 0. \tag{13a}$$

Similarly, the north-south mass transport is

$$\bar{M}_y = - \frac{R}{2\omega} \frac{\partial}{\partial y} \left[\bar{\tau}_x - \frac{\Delta P}{\Delta x} \right], \quad \varphi = 0. \tag{13b}$$

If lateral friction and acceleration are not negligible in the vicinity of the equator, then equations (13a, b) are rigorous only if the former quantities are constant or attain an extreme value at $\varphi = 0$.

The above equations serve as an independent means of checking the expressions involving stress only.

WIND STRESS THEORY

The expression used for calculating the stress of the wind, $\tau\ (txy)$, is

$$\tau\ (txy) = \rho' \gamma^2 u^2 , \tag{14}$$

where ρ' is the density of the air at sea level, $u = u\ (txy)$ is the wind speed at a fixed height, and γ^2 is the resistance coefficient, a nondimensional parameter. In general γ^2 is a function of the roughness of the surface and of the height at which the wind speed is measured. Rossby and Montgomery (1935), Rossby (1936b), and Munk (1947) have shown that a discontinuity in roughness occurs at a wind force of about 4 Beaufort. Assuming that the estimated wind velocity applies to a height of 8 meters, the values of the resistance coefficient above and below the critical wind speed are approximately:

$$\gamma_1^2 = 0.8 \times 10^{-3},\ u < \text{Beaufort } 4\,,$$
$$\gamma_2^2 = 2.6 \times 10^{-3},\ u > \text{Beaufort } 4\,.$$

These values, adopted by Sverdrup, *et al.* (1942), hold strictly for air of indifferent stability. It will be assumed here that the temperature lapse rate over the equatorial Pacific, on the average, equals that at indifferent equilibrium.

As indicated by Montgomery and Palmén (1940), because of the quadratic relationship between τ and u, the variability of the wind must be properly considered in evaluating the mean stress exerted by the wind. The complex variability of the wind velocity can be examined according to magnitude fluctuation and directional variation independently. The effect of variable magnitude is treated theoretically below.

The variability of wind speed in the *trade wind region* is assumed to be such that the distribution of *magnitude* about the mean, for any given direction and position, can be closely approximated by the Guassian law of error. At low mean speed the actual distribution probably becomes asymmetrical, which is contrary to the normal Guassian curve; but this fact is not important, since the stress exerted by a weak wind is exceedingly small.

In the following analysis, it is implied that the surface roughness is a discontinuous function of the wind speed. The critical speed is taken as 670 cm/sec.

For a Guassian distribution, the time mean of the stress, $\tau\,(xy)$, in any specified direction, is given by the expression

$$\tau\,(xy) = \frac{\rho' \int_{-\infty}^{\infty} \gamma^2 u^2 f\, ds}{\int_{-\infty}^{\infty} f\, ds}, \tag{15}$$

where the frequency f and the parameter s are defined as follows:

$$f = \frac{1}{\sqrt{2\pi}}\, exp\,(-\, s^2/2)\,, \tag{16a}$$

and

$$s = \frac{u - \bar{u}}{\sigma}. \tag{16b}$$

In (16), $\bar{u} = \bar{u}\,(xy)$ is the time mean of wind speed, and σ is the standard deviation of u.

The denominator of (15) is unity, so that in the special case where $\bar{u} = 670$ cm/sec, the equation takes the form

$$\tau\,(xy) = \rho' \left[\gamma_1^2 \int_{-\infty}^{0} u^2 f\, ds + \gamma_2^2 \int_{0}^{\infty} u^2 f ds \right]. \tag{17}$$

Inserting the expressions for f and u in terms of s, from (16), it follows that

$$\tau\,(xy) = \frac{\rho'}{\sqrt{2\pi}} \Big\{ (\gamma_1^2 + \gamma_2^2) \Big[\sigma^2 \int_{0}^{\infty} s^2 exp\,(-\, s^2/2)\, ds + \bar{u}^2 \int_{0}^{\infty} exp\,(-s^2/2)\, ds \Big] + (\gamma_2^2 - \gamma_1^2)\, 2\sigma\bar{u} \int_{0}^{\infty} s\; exp\,(-s^2/2)\, ds \Big\}. \tag{18}$$

Upon evaluation of the definite integrals, (18) simplifies to

$$\tau\,(xy) = \rho' \left[\frac{\gamma_1^2 + \gamma_2^2}{2} (\bar{u}^2 + \sigma^2) + (\gamma_2^2 - \gamma_1^2) \frac{2\sigma\bar{u}}{\sqrt{2\pi}} \right]. \tag{19}$$

Equation (19) applies strictly to the unique distribution whose mean is force 4 Beaufort. With slight modification (19) can be applied to other distributions. If σ is small enough, say ½ Beaufort interval, then at least 97 per cent of the distribution associated with a mean wind of either Beaufort 3 or 5 lies on the lower or higher side, respectively, of the critical speed (Fig. 6). Consequently, if γ_1^2 and γ_2^2 are replaced by the appropriate single value of γ^2, (19) will yield the stress with good approximation for any distribution whose mean is removed by at least 2σ from the critical speed.

With $\rho' = 1.16 \times 10^{-3}$ gm/cm³ (corresponding to air at 25° C and 1000 mb pressure), the equations of stress are (for $\sigma \leq \frac{1}{2}$ Beaufort interval):

$$\tau\,(xy) = 0.9 \times 10^{-6}(\bar{u}^2 + \sigma^2), \qquad \bar{u} \leqq 3 \text{ Beaufort}, \qquad (20a)$$

$$\tau\,(xy) = 2.0 \times 10^{-6}(\bar{u}^2 + 0.85\,\bar{u}\sigma + \sigma^2), \qquad \bar{u} = 4 \text{ Beaufort}, \qquad (20b)$$

$$\tau\,(xy) = 3.0 \times 10^{-6}(\bar{u}^2 + \sigma^2), \qquad \bar{u} \geq 5 \text{ Beaufort}, \qquad (20c)$$

where $\bar{u}$ and σ are in cm/sec and τ is in dynes/cm².

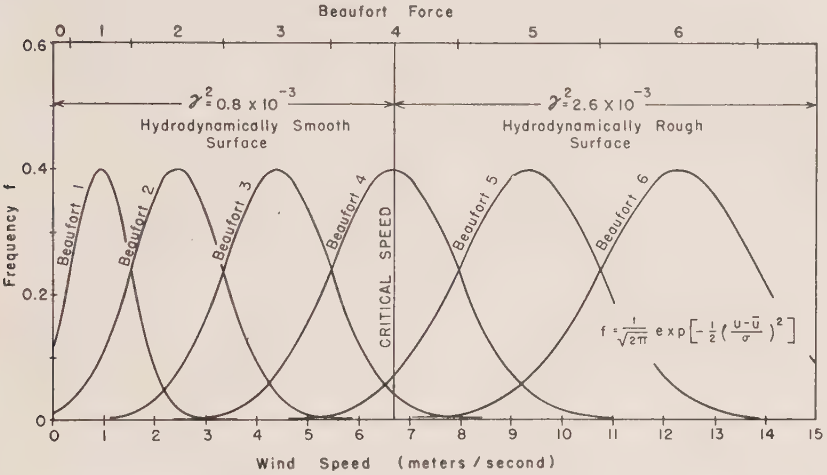

Figure 6. Assumed frequency distribution of wind speed for each integer Beaufort number of mean wind speed in the equatorial Pacific. The standard deviation of wind speed is ½ Beaufort interval. The sea surface roughness is indicated.

The value of σ was estimated for various values of wind speed in the trade wind area, and in each case it was found to be approximately ½ Beaufort interval (indicating an increase in the magnitude of σ in cm/sec with increase in mean wind speed). The wind stresses for each integer Beaufort number of mean speed in the trade wind area (Table I) have been calculated on the basis of this estimate and equations (20), using the velocity conversions of the *Smithsonian Tables*. Stresses for $\sigma = 0$ are included for comparison.

COMPUTATIONS

Because of the paucity of wind observations for the periods during which the oceanic data were obtained, it is necessary to turn to climatological statistics to obtain an accurate description of the distribution of wind. The data consist essentially of sixteen and eight sector wind roses from the October and November *Pilot Charts* (U. S. Hydrographic Office, 1946) and the September-October-November *Pilot Chart* (U. S. Hydrographic Office, 1942) for the Pacific. Wind roses are given for each five degree square, such that a total of 83 are included within the area concerned.

The available oceanographic observations consist principally of two sections running roughly north–south: section A, *Carnegie* stations 147 to 159 (Fleming, *et al.*, 1945), occupied from October 15 to October 29, 1929, running from 138° 14′ W, 27° 27′ N to 159° 01′ W, 9° 24′ S; and section B, *Carnegie* stations 35 to 46, representing the period from October 26 to November 21, 1928, and *Bushnell* stations 307 to 299 (Sverdrup, *et al.*, 1943), occupied from March 18 to March 25, 1939, extending from 111° 25′ W, 22° 23′ N to 108° 20′ W, 9° 06′ S. In addition, two parallel sections are included: *Bushnell* stations 309 to 315, extending from 124° 13′ W, 29° 40′ N to 149° 35′ W, 20° 44′ N, and *Carnegie* stations 131 to 137, from 126° 20′ W, 33° 49′ N to 145° 33′ W, 24° 02′ N, for April 1939 and September 1929, respectively. Fig. 13 shows the position of these stations. Values of ΔD for each station are tabulated in the reports cited.

TABLE I—ASSIGNMENT OF WIND STRESS FOR THE TRADE WIND REGION*

Beaufort number of mean wind	*Velocity Range (mps)*	*Velocity $\bar{u}$ (cm/sec)*	*Stress, τ, dynes/cm²*	
			$\sigma = 0$	$\sigma = \frac{1}{2}$ *Beauf. int.*
1	0.4– 1.5	95	.01	.01
2	1.6– 3.3	245	.06	.06
3	3.4– 5.4	440	.18	.19
4	5.5– 7.9	670	.89	1.06
5	8.0–10.7	935	2.65	2.70
6	10.8–13.8	1230	4.60	4.65
7	13.9–17.1	1550	7.25	7.30
8	17.2–20.7	1890	10.80	10.85

* The stress calculated on the basis of no standard deviation of wind speed has been included in the table (first stress column) for comparison with the values calculated for the trade wind area ($\sigma = \frac{1}{2}$ Beaufort interval).

Wind Stress Computations. The stresses for each direction of the wind roses were evaluated by use of Table I, according to the indicated Beaufort number. Each stress was in turn weighted according to its frequency of occurrence, and broken down into east and north components. The sum of each set of weighted components divided by the total frequency gave the components of mean stress. A summary of the computed stress components is presented in Tables II and III for October and November, respectively.

It is apparent from the change in sign of τ_y that a well defined convergence of stress is present between 7½° N and 12½° N, in agreement with the convergence of mean wind streamlines analyzed by Werenskiold (1922). Zones of maximum magnitude of stress are evident at about 5° S and 17½° N, except near the continent, where the picture is obscured by the influence of the land.

The values of mean stress $\bar{\tau}_x$ and $\bar{\tau}_x'$ were computed for the two months using sections A and B as the arbitrary boundaries x_1 and x_2, respectively, in the averaging process. The October-November mean wind stress distribution was taken as representative of actual conditions existing at the time of the oceanographic observations (excluding *Bushnell* data). The computed two-month averages are shown in Fig. 7. Values of τ_y were determined from the stresses along section A (for a 10° band of longitude). The October-November mean τ_y curve is given in Fig. 8.

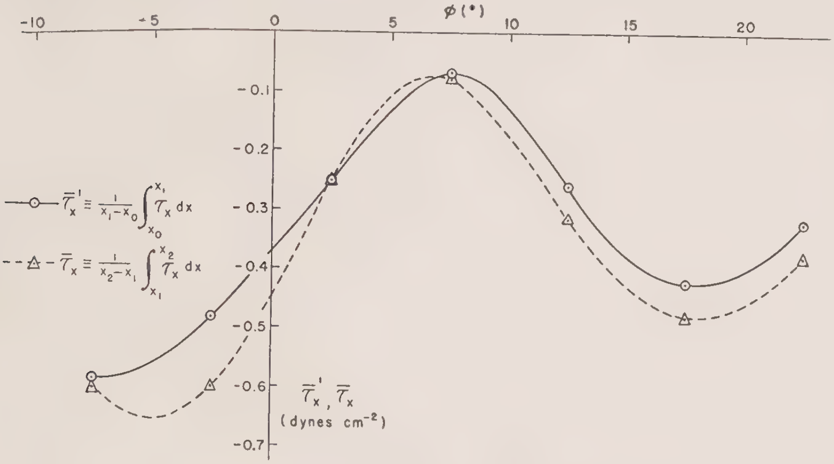

Figure 7. Latitude dependence of the mean east–west wind stress components, $\bar{\tau}_x$ and $\bar{\tau}_x'$ The curves represent climatological average stresses for the period October 1 to November 30

The mean longitudinal stress curves represent a total of more than 3000 observations each (U. S. Weather Bureau, 1938). The shape of these curves suggests a sinusoidal distribution of the form

$$\tau_x = \tau_0 + a\,(\varphi - \varphi_0) + b \sin 2k\,(\varphi - \varphi_0)\,, \qquad (21)$$

which would make possible an analytic solution. This will be discussed later.

TABLE II—SUMMARY OF COMPUTED WIND STRESSES—OCTOBER

τ_x and τ_y are given in the numerator and denominator, respectively, of the tabulated fractions, the units being dynes/cm^2.

Lat. (°)	*Longitude—West*														
	152.5	147.5	142.5	137.5	132.5	127.5	122.5	117.5	112.5	107.5	102.5	97.5	92.5	87.5	82.5
22.5	—	—	—	$\frac{-.70}{-.39}$	$\frac{-.66}{-.55}$	$\frac{-.50}{-.43}$	$\frac{-.39}{-.45}$	$\frac{-.20}{-.30}$	$\frac{.08}{-.13}$	$\frac{.04}{-.03}$	—	—	—	—	—
17.5	—	—	—	$\frac{-.79}{-.64}$	$\frac{-.68}{-.40}$	$\frac{-.58}{-.59}$	$\frac{-.51}{-.34}$	$\frac{-.30}{-.30}$	$\frac{-.04}{-.17}$	$\frac{.02}{-.05}$	$\frac{-.02}{.01}$	—	—	—	—
12.5	—	—	—	$\frac{-.63}{-.44}$	$\frac{-.39}{-.26}$	$\frac{-.37}{-.21}$	$\frac{-.17}{-.11}$	$\frac{-.06}{-.01}$	$\frac{.08}{-.08}$	$\frac{.10}{.00}$	$\frac{.12}{.11}$	$\frac{-.04}{-.32}$	$\frac{.03}{-.01}$	$\frac{.03}{.02}$	—
7.5	—	—	$\frac{-.34}{.26}$	$\frac{-.24}{.11}$	$\frac{-.31}{.38}$	$\frac{-.11}{.30}$	$\frac{.08}{.27}$	$\frac{.19}{.67}$	$\frac{.17}{.66}$	$\frac{.16}{.60}$	$\frac{-.15}{.40}$	$\frac{.35}{.23}$	$\frac{.46}{.57}$	$\frac{.10}{.03}$	$\frac{.12}{.03}$
2.5	—	$\frac{-.55}{.31}$	$\frac{-.40}{.36}$	$\frac{-.62}{.31}$	$\frac{-.68}{.45}$	$\frac{-.65}{.58}$	$\frac{-.55}{.77}$	$\frac{-.45}{.81}$	$\frac{-.12}{.56}$	$\frac{.01}{.51}$	$\frac{-.17}{.64}$	$\frac{.02}{.45}$	$\frac{.14}{.58}$	$\frac{.34}{.84}$	$\frac{.19}{.42}$
−2.5	$\frac{-.50}{-.09}$	$\frac{-.50}{.04}$	$\frac{-.73}{.14}$	$\frac{-.49}{.21}$	$\frac{-1.21}{.02}$	$\frac{-.85}{.30}$	$\frac{-.88}{.40}$	$\frac{-.52}{.20}$	$\frac{-.55}{.29}$	$\frac{-.53}{.37}$	$\frac{-.21}{.13}$	$\frac{-.08}{.08}$	$\frac{-.07}{.10}$	$\frac{-.06}{.27}$	$\frac{.05}{.17}$
−7.5	$\frac{-.21}{.03}$	$\frac{-.67}{-.20}$	$\frac{-.28}{.11}$	$\frac{-.33}{.21}$	$\frac{-.85}{.12}$	$\frac{-.84}{.18}$	$\frac{-.83}{.28}$	$\frac{-.84}{.30}$	$\frac{-.68}{.37}$	$\frac{-.52}{.22}$	$\frac{-.53}{.52}$	$\frac{-.63}{.40}$	$\frac{-.64}{.49}$	$\frac{-.50}{.69}$	$\frac{-.49^*}{.54}$

* All values for −7.5° Latitude are September–October–November mean values (1942 *Pilot chart*).

TABLE III—SUMMARY OF COMPUTED WIND STRESSES—NOVEMBER

τ_x and τ_y are given in the numerator and denominator, respectively, of the tabulated fractions, the units being dynes/cm^2.

Lat. (°)	*Longitude—West*														
	152.5	147.5	142.5	137.5	132.5	127.5	122.5	117.5	112.5	107.5	102.5	97.5	92.5	87.5	82.5
22.5	—	—	—	$\frac{-.50}{-.47}$	$\frac{-.57}{-.33}$	$\frac{-.44}{-.43}$	$\frac{-.42}{-.44}$	$\frac{-.31}{-.35}$	$\frac{.06}{-.12}$	$\frac{.03}{-.11}$	—	—	—	—	—
17.5	—	—	—	$\frac{-1.03}{-.53}$	$\frac{-.90}{-.55}$	$\frac{-.60}{-.41}$	$\frac{-.71}{-.53}$	$\frac{-.58}{-.51}$	$\frac{-.04}{-.11}$	$\frac{.03}{-.10}$	$\frac{.00}{-.03}$	—	—	—	—
12.5	—	—	—	$\frac{-.69}{-.43}$	$\frac{-.62}{-.34}$	$\frac{-.69}{-.54}$	$\frac{-.50}{-.21}$	$\frac{-.54}{-.24}$	$\frac{-.79}{-.27}$	$\frac{-.16}{-.03}$	$\frac{-.05}{-.03}$	$\frac{-.29}{-.71}$	$\frac{-.01}{-.05}$	$\frac{-.08}{-.09}$	—
7.5	—	—	$\frac{-.48}{.01}$	$\frac{-.58}{.06}$	$\frac{-.37}{.21}$	$\frac{-.22}{.23}$	$\frac{-.10}{.14}$	$\frac{-.01}{.12}$	$\frac{-.02}{.12}$	$\frac{-.19}{.15}$	$\frac{-.24}{.27}$	$\frac{.01}{.25}$	$\frac{-.08}{.15}$	$\frac{.00}{-.05}$	$\frac{.10}{.04}$
2.5	—	$\frac{-.53}{.39}$	$\frac{-.51}{.21}$	$\frac{-.43}{.40}$	$\frac{-.22}{.40}$	$\frac{-.61}{.73}$	$\frac{-.54}{.76}$	$\frac{-.46}{.72}$	$\frac{-.27}{.47}$	$\frac{-.28}{.50}$	$\frac{-.09}{.43}$	$\frac{-.17}{.25}$	$\frac{.07}{.38}$	$\frac{.33}{.52}$	$\frac{.09}{.14}$
−2.5	$\frac{-.52}{-.06}$	$\frac{-1.02}{-.04}$	$\frac{-.51}{-.03}$	$\frac{-1.05}{.14}$	$\frac{-.79}{.34}$	$\frac{-.89}{.33}$	$\frac{-.81}{.47}$	$\frac{-.76}{.41}$	$\frac{-.64}{.31}$	$\frac{-.29}{.06}$	$\frac{-.08}{.09}$	$\frac{-.06}{.08}$	$\frac{-.02}{.06}$	$\frac{-.04}{.16}$	$\frac{.07}{.15}$
−7.5	(See Table II)														

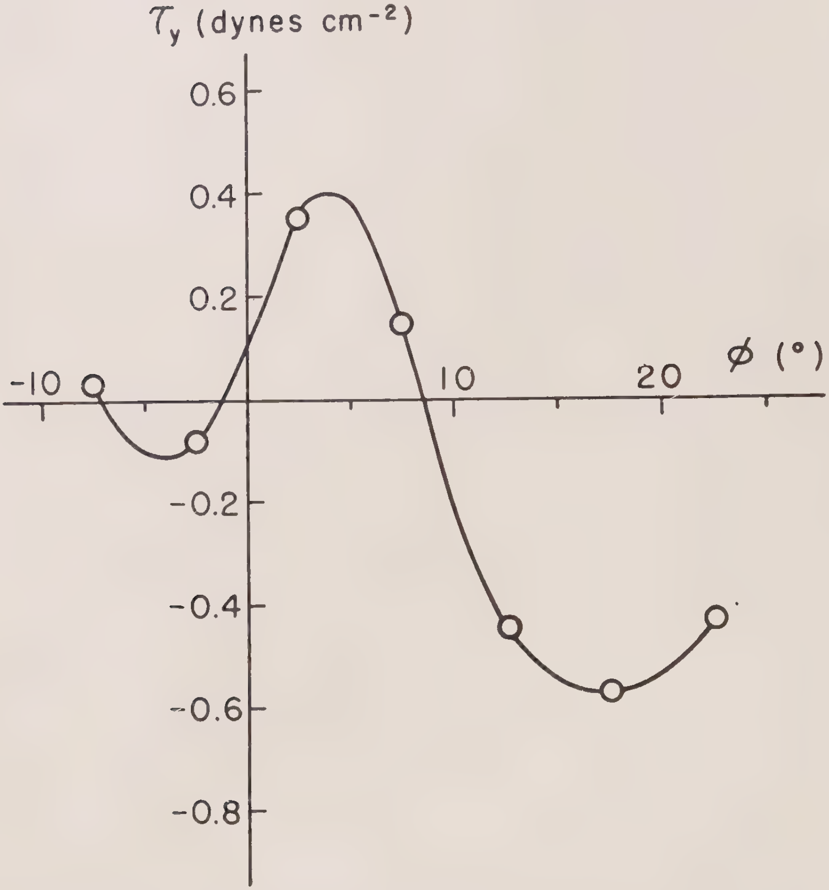

Figure 8. Plot of the north–south stress component, τ_y. The curve represents the October-November mean for a band ten degrees wide along the section A.

Using the values of $\bar{\tau}_x$ (Fig. 7), together with its numerically determined derivatives, the evaluation of the function $f_1(\tau)$ by expression (8) was carried out for each degree of latitude between 8° S and 22° N (Fig. 9). Applying (9), the function $f_4(\tau)$ was evaluated for the same range (Fig. 12). The values of $\bar{\tau}_x'$, together with the numerically determined second derivatives of $\bar{\tau}_x'$, were used to compute the stress functions $f_2(\tau)$ and $f_3(\tau)$ by equations (6) and (7), respectively (Figs. 10, 11).

Oceanographic computations. The values of P for each of the 47 stations (Table IV) were derived from equation (11) by numerical integration, using twelve standard depth intervals. The values of d and $\bar{\rho}$ were taken as 1000 m and unity, respectively, and the constant was arbitrarily set equal to zero.

A considerable discrepancy in P between the *Carnegie* and *Bushnell* stations is evident from the values of the nearly coincident runs C131 to 137 and B309 to 315 (Table IV). At a point in common with the two runs, near stations B312 and C148, it is found that the *Carnegie* value is 2.2×10^8 dynes/cm. in excess of that of the *Bushnell.*

A comparison of salinity values at great depth of the *Carnegie* cruise with those of other expeditions indicates that the former are consistently 0.03 parts per mille too low (Wüst, 1935; Schott, 1935; and Sverdrup, *et al.*, 1944). This leads to an error in P which is of the same sign and about the same magnitude as that found above.

TABLE IV—List of Stations and Integrated Pressure

Sta.	*Lat.*	*Long.*	*P*	*P′*	*Sta.*	*Lat.*	*Long.*	*P*	*P′*
	° ′	° ′	*	*		° ′	° ′	*	*
C131	33 49	126 20	57.1	0.9	B309	29 40	124 13	52.5	−1.5
132	31 38	128 48	58.6	2.4	310	28 26	128 32	54.4	0.4
133	29 21	132 30	61.6	5.4	311	27 01	132 51	57.8	3.8
134	27 45	135 22	60.9	4.7	312	25 22	137 12	59.5	5.5
135	26 39	139 07	61.3	5.1	313	23 55	141 07	60.1	6.1
136	26 13	142 02	62.1	5.9	314	22 29	144 50	60.0	6.0
137	24 02	145 33	63.2	7.0	315	20 44	149 35	60.0	6.0
147	27 27	138 14	61.1	4.9	307	22 23	111 25	54.4	0.4
148	24 57	137 44	62.0	5.8	306	20 46	109 21	52.9	−1.1
149	21 18	138 36	63.0	6.8	305	20 00	108 16	53.6	−0.4
150	16 15	137 06	56.4	0.2	304	18 34	106 23	52.8	−1.2
151	12 40	137 32	55.2	−1.0	303	17 43	105 16	54.0	0.0
152	10 05	139 44	54.3	−1.9	302AB	15 39	101 50	53.3	−0.7
153	7 45	141 24	56.7	0.5	302	13 55	99 00	58.1	4.1
154	6 42	143 22	57.8	1.6	299	9 02	86 50	52.5	−1.5
155	4 51	146 46	59.3	3.1	C 35	6 32	80 04	53.4	−2.8
156	3 01	149 46	60.1	3.9	37	5 59	82 56	55.6	−0.6
157	−1 48	152 22	58.1	1.9	38	3 46	81 37	55.6	−0.6
158	−6 33	154 58	59.5	3.3	36	2 54	80 02	58.1	1.9
159	−9 24	159 01	61.6	5.4	39	0 52	81 14	56.4	0.2
					40	−1 32	82 16	57.0	0.8
					41	−1 37	86 58	54.4	−1.8
					42	−1 32	93 10	55.5	−0.7
					43	−2 30	95 43	54.6	−1.6
					44	−3 15	99 48	54.2	−2.0
					45	−4 35	105 03	54.0	−2.2
					46	−9 06	108 20	56.1	−1.1

C = *Carnegie* stations

B = *Bushnell* stations

P = Integrated pressure computed directly from oceanographic data, using equation (11).
P' = Integrated pressure on an arbitrary scale, adjusted for a discrepancy of 2.2×10^8 dynes/cm between *Carnegie* and *Bushnell* data.

* All values of P and P' are given in units of 10^8 dynes/cm.

In order that the *Carnegie* data be compatible with the *Bushnell*, the quantity 2.2 × 10^8 dynes/cm was substracted from each of the *Carnegie* values of *P*. The final values of integrated pressure, *P′*, in Table IV have been shifted to an arbitrary scale by reducing all values of *P* by 54.0 × 10^8 dynes/cm. This shift has no effect upon the gradient of *P*, but it makes possible a direct comparison of computed *P* with that found by the analytic solution to be discussed later.

A semiobjective procedure was followed in evaluating the average gradient of *P* in the *x* direction. Since the values of *P* for section A form a remarkably smooth curve (Fig. 10), the differences, Δ*P*, be-

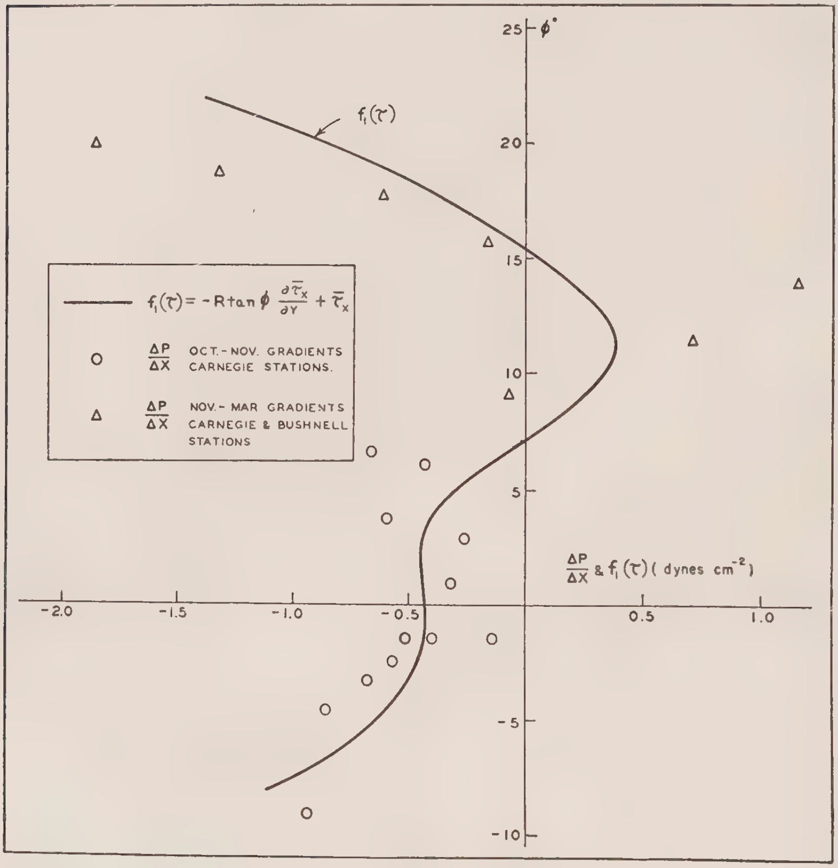

Figure 9. Plot of theoretical and observed values of $\Delta P/\Delta x$, betweeen sections A and B, as a function of latitude.

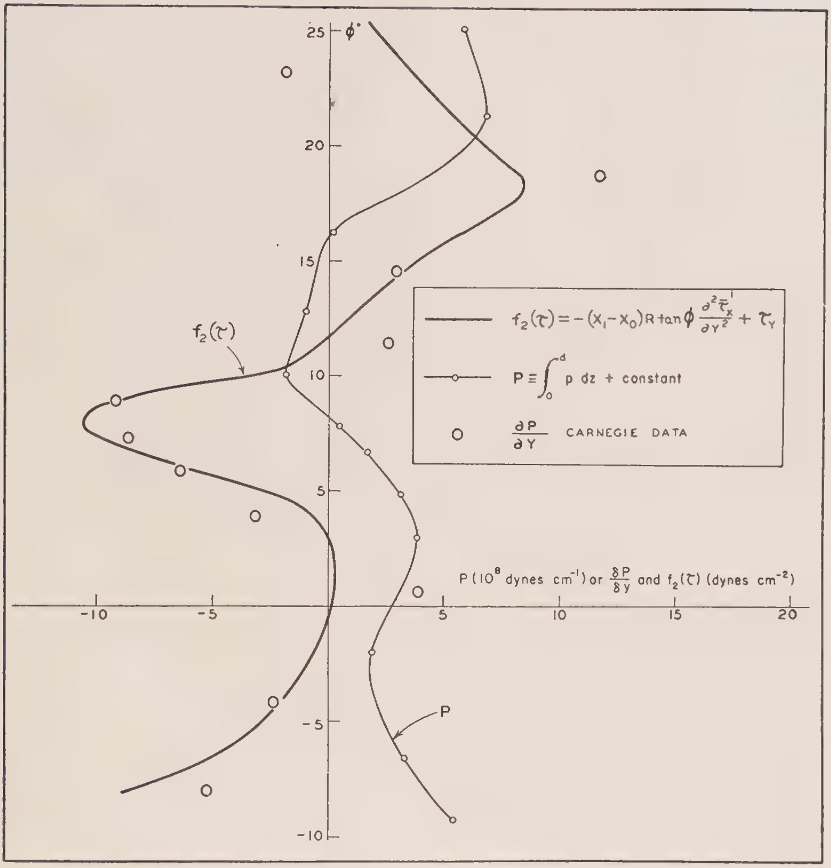

Figure 10. Plot of theoretical and observed values of $\partial P/\partial y$ as a function of latitude. Observed values have been evaluated from the *Carnegie* data along section A. Values of P for each station of section A are included.

tween the sections were computed at latitudes corresponding to those of the stations of the eastern section. Interpolation was necessary at section A only. Values of Δx were found in a similar manner, and several values of $\Delta P/\Delta x$ derived (Fig. 9).

Section A was used to obtain discrete values of the north–south gradient of P between stations. In determining the approximations of $\partial P/\partial y$, account was taken of the fact that this section is not truly north–south. The gradient is given by the following approximation:

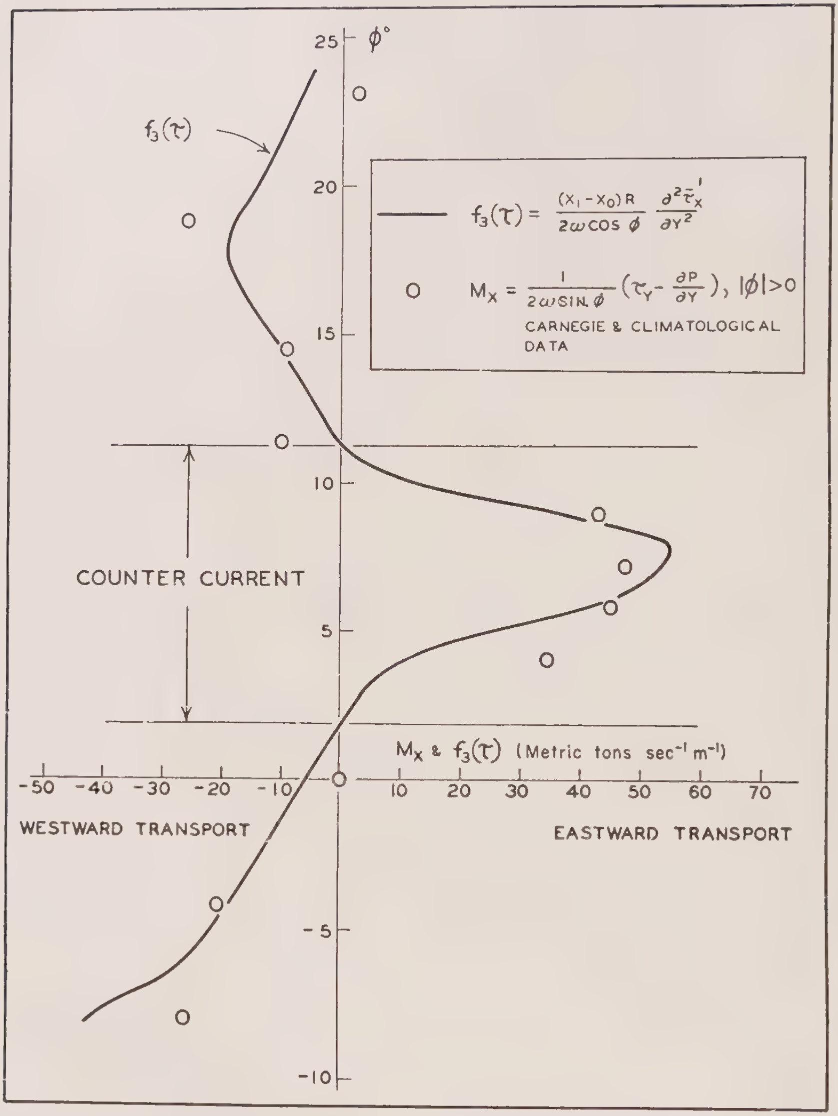

Figure 11. Latitude dependence of the longitudinal mass transport, M_x, computed by two independent methods. M_x represents the net eastward transport of water in tons per second through a column of 1000 meters depth and 1 meter width, at the *Carnegie* path (section A).

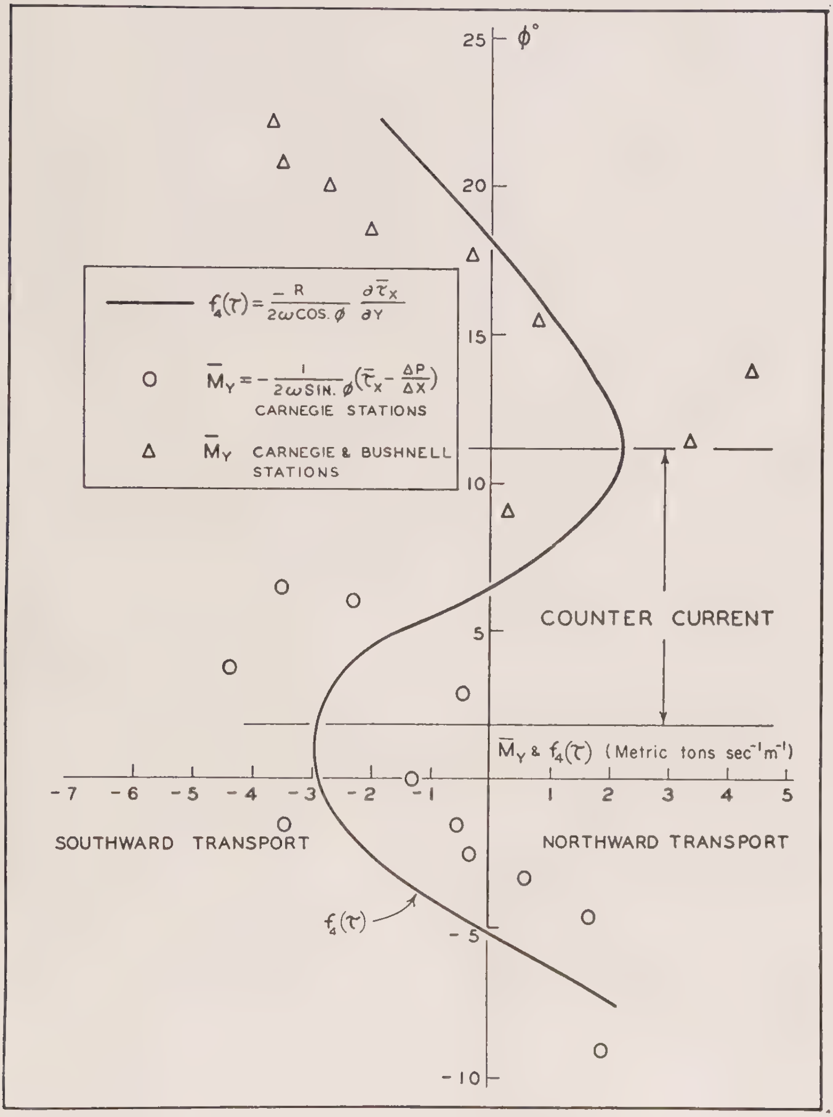

Figure 12. Latitude dependence of the latitudinal mass transport, $\bar{M}_y$, computed by two independent methods. $\bar{M}_y$ represents the mean net northward transport of water in tons per second through a column of 1000 meters depth and 1 meter width, between the two sections A and B.

$$\frac{\partial P}{\partial y} = \frac{\Delta P}{\Delta y} - \frac{\partial P}{\partial x}\frac{1}{\tan \varphi}, \tag{22}$$

where $\Delta P = \Delta P\,(x_1\,y)$ is the difference of P between adjacent stations, Δy is the corresponding change of y, and β is the bearing of the path. The gradient $\partial P/\partial x$ was approximated by $\Delta P/\Delta x$ in the determination of the final north–south gradient of P (Fig. 10).

The values of $\Delta P/\Delta x$ and $\partial P/\partial y$ for latitudes, $|\varphi|$, greater than 1° were employed in computing M_x and $\bar{M}_y$ by means of (12). Values within one degree of the equator were used in conjunction with adjacent values of the gradients to determine the second derivatives of P at the equator. This afforded means of computing the transport at the equator by (13). The resulting values are plotted in Figs. 11 and 12.

ANALYTIC SOLUTION

The essential features of the horizontal distribution of transport and of mass in the equatorial Pacific can be recognized most readily by an examination of the following simple wind stress distribution:

$$\tau_x(y) = \tau_0 + b \sin 2k\,(\varphi - \varphi_0)\,, \tag{23a}$$

and

$$\tau_y(y) = \; - c \sin k\,(\varphi - \varphi_0')\,, \tag{23b}$$

where τ_0, b, c, k, φ_0, and φ_0' are constants. Equation (23a) is a special case of (21).

The boundary is approximated [for the range $-15° \leqslant \varphi \leqslant 35°$] by the analytic function:

$$x_0(y) = L - my + n \sin 2K\,(\varphi - \varphi_0'')\,, \tag{24a}$$

or

$$\tan \theta = \frac{dx_0}{dy} = -m + \frac{2Kn}{R} \cos 2K\,(\varphi - \varphi_0'')\,, \tag{24b}$$

where L, m, n, K, and φ_0'' are constants.

Equations (1) and (5), together with the expressions (23) and (24), determine an analytic function $P = F\,(xy)$. The complete solution can be shown to be:

$$F(xy) = \tau_0 x + \Big[x - x_0(y)\Big]\Big\{b \sin 2k(\varphi - \varphi_0) - 2kb \cos 2k(\varphi - \varphi_0) \tan \varphi\Big\}$$
$$+ \frac{cR}{k} \cos k(\varphi - \varphi_0') + \frac{bRm}{2k} \cos 2k(\varphi - \varphi_0)$$

$$+ \frac{bnK}{(k^2 - K^2)} \left[K \cos 2k(\varphi - \varphi_0) \cos 2K(\varphi - \varphi_0'') \right.$$
$$\left. + K \sin 2k(\varphi - \varphi_0) \sin 2K(\varphi - \varphi_0'') \right], \qquad (25)$$

provided that $k^2 \neq K^2$. The constant of integration is arbitrarily set equal to zero.

It can be further verified that the mass transport components, satisfying equations (4), (5), (23), and (24), are given by the expressions:

$$M_x = - \frac{2k^2 b}{\omega R} \frac{[x - x_0(y)] \sin [2k(\varphi - \varphi_0) - \alpha]}{\cos \varphi \cos \alpha}$$
$$+ \frac{kb}{\omega} \frac{\cos 2k(\varphi - \varphi_0)}{\cos \varphi} \left[m - \frac{2Kn}{R} \cos 2K(\varphi - \varphi_0'') \right], \qquad (26a)$$

and
$$M_y = - \frac{kb}{\omega} \frac{\cos 2k(\varphi - \varphi_0)}{\cos \varphi}. \qquad (26b)$$

In (25) and (26) the term x replaces the term x_1 in the original equations. The angle α is a small fraction of φ, according to the relation

$$\tan \alpha = \frac{\tan \varphi}{2k}.$$

For $(x - x_0) \geqslant R$, the last three terms of (25) and the last term of (26a) are unimportant.

Since the field of mass is assumed stationary, implying that the mass transport is nondivergent, there exists a stream function, $\psi = \psi\,(xy)$, for which

$$\frac{\partial \psi}{\partial x} = - M_y, \quad \frac{\partial \psi}{\partial y} = M_x. \qquad (27)$$

In view of (26), the solution for ψ is

$$\psi = \frac{kb}{\omega} \left[x - x_0(y) \right] \frac{\cos 2k\,(\varphi - \varphi_0)}{\cos \varphi}. \qquad (28)$$

It can be shown that (28) holds for any boundary.

The transport of water between the surface and level d is parallel to the isolines of ψ, or streamlines, and the mass flowing per unit time between adjacent streamlines is equal to the corresponding difference in ψ.

The constants were taken as follows:

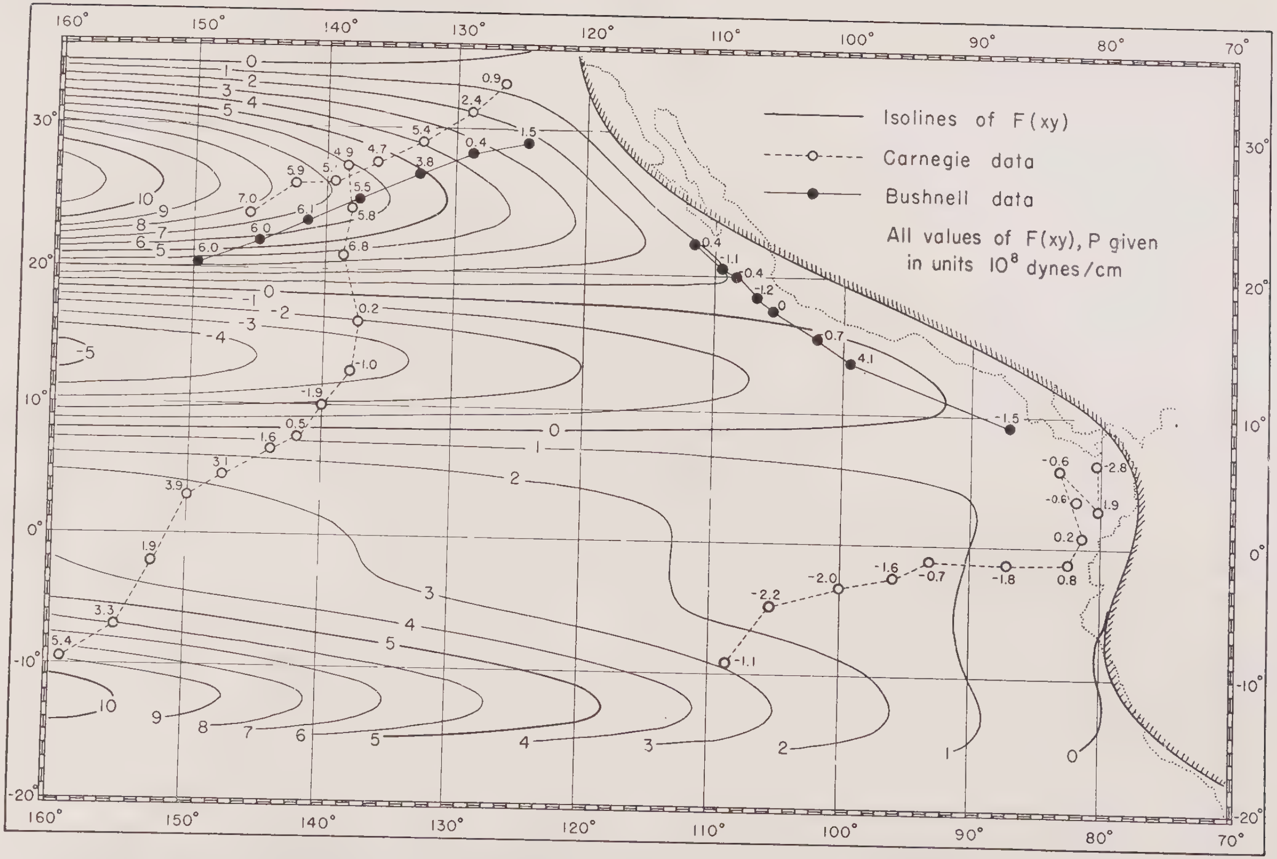
Isolines of F(xy)
Carnegie data
Bushnell data
All values of F(xy), P given in units 10⁸ dynes/cm
160° 150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° -10° -20°

Figure 13. The horizontal distribution of integrated pressure, $F(xy)$, based on a sinusoidal distribution of longitudinal wind stress and an hypothetical boundary (see p. 92). The values of adjusted integrated pressure, P', computed from oceanographic data, are plotted for comparison

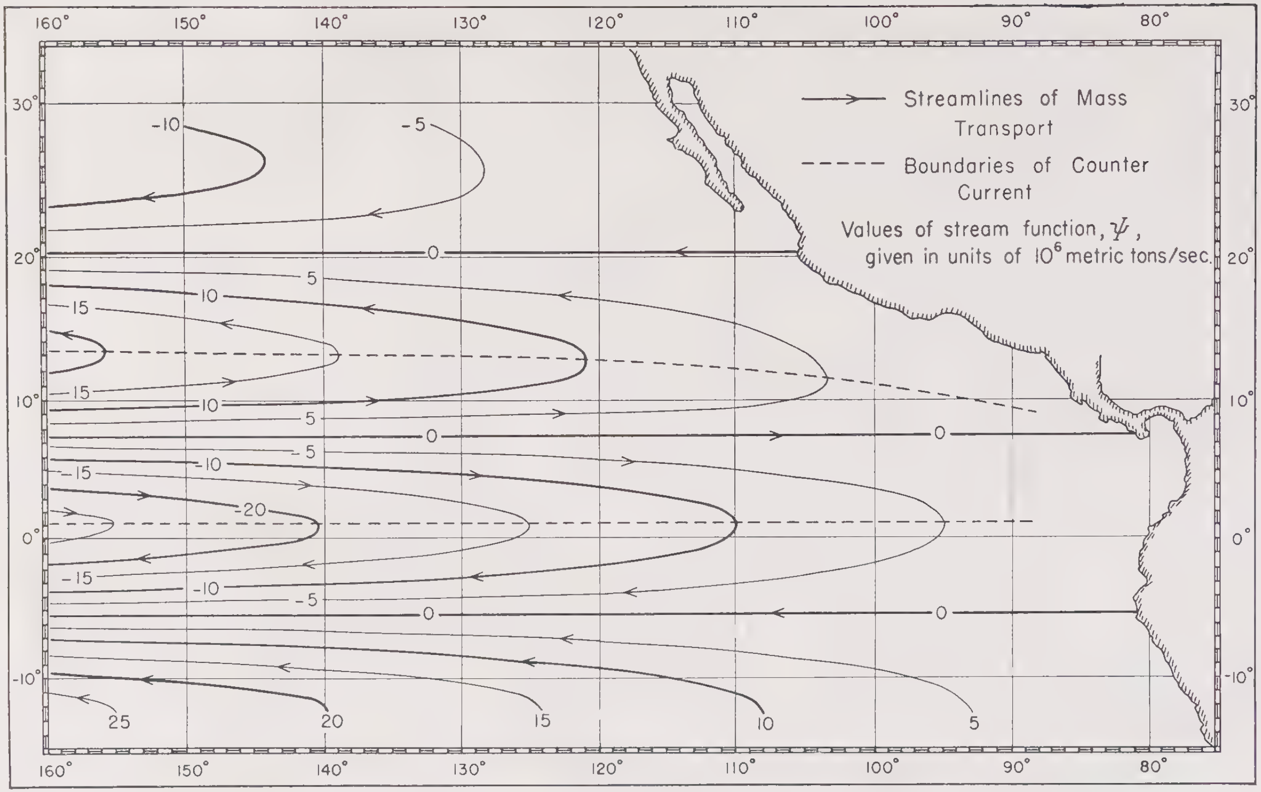
Streamlines of Mass Transport
Boundaries of Counter Current
Values of stream function, ψ, given in units of 10⁶ metric tons/sec.
160°
150°
140°
130°
120°
110°
100°
90°
80°
30°
20°
10°
0°
-10°
-10
-5
0
5
10
15
-15
-10
-5
0
-20
-5
-10
-15
0
25
20
15
10
5

Figure 14. Streamlines of flow, representing the field of mass transport, based on a sinusoidal stress distribution and the actual boundary. Values of the stream function, ψ, are indicated. Differences of ψ between streamlines represent the net mass in millions of tons flowing per second between those streamlines (from the surface to a depth of 1000 meters). The boundary represents a streamline for which $\psi = 0$.

$\tau_0 = -0.3$ dyne/cm², $m = 0.85$, $R = 6.37 \times 10^8$ cm,
$b = 0.3$ dyne/cm², $n = 9 \times 10^7$ cm, $\varphi_0 = 1°$,
$c = 0.4$ dyne/cm², $k = 180/26 = 6.923$, $\varphi_0' = \varphi_0 + 90°/2k = 7.5°$,
$L = 80°$ W longitude, $K = 180/40 = 4.500$, $\varphi_0'' = -2°$.

Values of $F(xy)$ from (25) were determined for the region from 160° W longitude to the analytic boundary (Fig. 13). These were compared with corresponding values of P, computed from oceanic data, enabling the reduction of P to a scale in common with F (xy). The adjusted values, $P' = P - 54.0 \times 10^8$ dynes/cm (Table IV), have been plotted in the horizontal distribution chart (Fig. 13). A coefficient of correlation of 0.73 between the analytic solution, F, and the values of P' is obtained for the stations cited.

The quantity $F(xy)$ or P has a physically clear meaning in the case of the simple two layer system, where a light homogeneous layer of thickness h overlies a heavier homogeneous layer at rest. In this case, it can be demonstrated (Defant, 1936) that P is a quadratic in h. For such a system then, h would increase with distance from the coast.

Fig. 14 is a plot of the stream function based on the true boundary. It can be seen that the total mass transport of the counter current across the 140th meridian, from the difference of ψ, is about 35 million tons per second. This is somewhat higher than found for both the oceanographic and actual stress data. The boundary represents a zero valued streamline, but not an isoline of F (xy).

DISCUSSION

Figs. 9 and 10 are similar to those discussed by Sverdrup (1947). Despite the fact that the oceanic data are meager, the curves show a remarkable agreement with the principal characteristics of those observations.

The comparison of the mass transports, computed by the two independent methods, is even more striking (Figs. 11, 12). The total mass transport of the equatorial counter current, between the surface and 1000 meters computed by numerical integration of f_3 (τ), is 26.7 million metric tons per second, across the *Carnegie* section. This compares well with the estimate of transport given by Sverdrup, *et al.* (1942), which is 25 million m³ per second between the surface and 700 meters, for the same section.

The limits of the counter current are at 2° N and 12° N latitude (Fig. 11), and are indicative of the mean width of the current for the 1000 meter column. However, because of the widening of the current with depth, indicated by the *Carnegie* profile (Sverdrup, *et al.*, 1942), the surface current should be of less width. In support of this, the October and November *Pilot Charts* (U. S. Hydrographic Office, 1946) show surface currents to the east in a band from about 5° N to 12° N.

From the plots of P (Figs. 10, 13) it is evident that the principal troughs and ridges are accounted for by the wind stress functions, except in the region of the equator, where the theory fails to describe the conspicuous rise of P to the north across the equator. It is possible that this anomolous pressure gradient could be maintained by thermodynamic processes in the vicinity of the equator. This is suggested by the fact that the observed maximum in P, just north of the equator, is almost coincident with the minimum in net evaporation given by Wüst (1936). It is clear that such a gradient, in excess of that which can be maintained by the stress of the wind at the equator, can be balanced only by lateral friction forces if unaccelerated motion is to prevail. For this reason, the picture of flow *in the vicinity of the equator* is not clear.

An alternate possibility is that the discrepancy mentioned above is not a real one. The mean atmospheric pressure distribution for October and November is asymmetrical with respect to the equator. This could bring about a discontinuity in longitudinal stress, and in turn a sharp rise of the function P across the equator. This is apparent if one considers the following approximation obtained from (1a) and (7):

$$P = (x_1 - x_0)\left(\bar{\tau}_x' - R \tan\varphi \frac{\partial \bar{\tau}_x'}{\partial y}\right) + \text{constant}. \tag{29}$$

This expression is meaningless at $\varphi = 0$, if $\bar{\tau}_x'$ is discontinuous, but at a very small distance from the equator the expression reduces to $(x_1 - x_0)\,\bar{\tau}_x'$. Accordingly, a sharp rise of but 0.2 dyne/cm^2 in $\bar{\tau}_x'$ across the equator could lead to a corresponding rise of P in the amount of 1.0×10^8 dyne/cm along the *Carnegie* section.

SUMMARY AND CONCLUSION

By ignoring lateral friction and thermodynamic processes, it has been verified that, in the eastern equatorial Pacific, the predominant features of the distribution of mass and of mass transport of water can be accounted for semiquantitatively in terms of the wind stress alone.

The longitudinal mass transport increases nearly linearly with distance from the continent, while the north–south transport is practically independent of longitude and is a maximum very near the boundaries of the counter current.

The principal discrepancy of theory and observation exists in the proximity of the equator, where it is possible that thermodynamic processes and lateral friction are important. This discrepancy may not be real but may be brought about because of insufficient details of wind stress near the equator.

No attempt has been made to describe the vertical distribution of mass; such an analysis is to be presented in a forthcoming paper.

ACKNOWLEDGMENT

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Contribution No. 354

Hindcasting Technique Provides Statistical Wave Data

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IN THE PAST it has rarely been possible to base the design of structures affected by wave action upon quantitative estimates of essential wave characteristics, such as height, period, and direction. Consequently some structures have failed to produce the desired results, and some have collapsed under the action of the waves. Also, material and construction time have been wasted on structures designed to withstand far greater wave action than they will ever encounter.

Shoreline and beach-profile changes are due partially to the movement of sand by the orbital motion of the water in waves and partially to sand transport by longshore currents. Prevailing and extreme wave conditions are basic factors used in applying recently developed theories to obtain quantitative estimates of sand movement.

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The value of a projected breakwater depends upon its sheltering effect and its effect upon longshore currents and sand transport. Statistical wave data aid in determining the desirability of the proposed plan and in amending it, if necessary, before construction is undertaken. In harbor planning based on model studies, statistical wave data are utilized in calculating the dimensions of the waves used in the model.

During the war a method of forecasting wave characteristics along

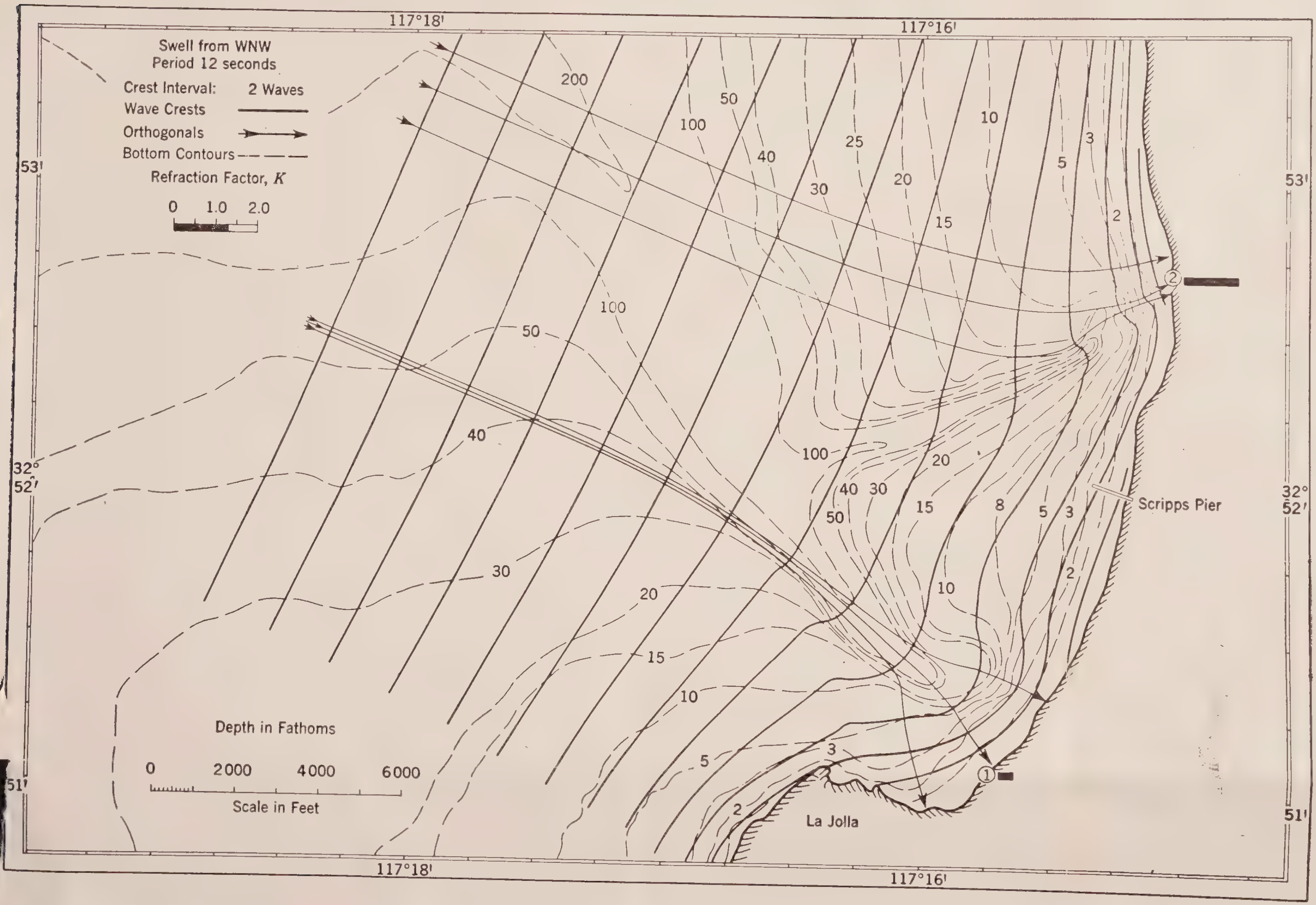
117°18'
117°16'
Swell from WNW
Period 12 seconds
Crest Interval: 2 Waves
Wave Crests
Orthogonals
Bottom Contours
Refraction Factor, K
0 1.0 2.0
53'
32° 52'
51'
200
100
50
40
30
25
20
15
10
8
5
3
2
②
①
Scripps Pier
La Jolla
Depth in Fathoms
0 2000 4000 6000
Scale in Feet

FIG. 1. SIMPLIFIED REFRACTION DIAGRAM for Scripps Beach 16 miles north of San Diego, Calif., illustrates effects of submarine canyon off Sta. 1 and submarine ridge off Sta. 2 on wave divergence and height of breakers.

beaches where amphibious landings were to take place was developed by the Scripps Institution of Oceanography and the Department of Engineering, University of California, and the Woods Hole Oceanographic Institution under contract with the U.S. Navy and War Departments. Complete treatment of the theory and forecasting techniques used can be found in publications of the U.S. Hydrographic Office.

As first suggested by Dr. H. U. Sverdrup, then Director of Scripps Institution of Oceanography, wave forecasting techniques can be applied to the computation of wave characteristics by using historical weather maps which are now available for the Northern Hemisphere for a period of 40 years prior to 1939. In brief, the characteristics of waves arriving at a point in deep water offshore may be computed from quantities which are readily obtained from weather maps. These quantities are the wind velocity, the wind duration, and the size and position of the area over which the wind blows.

Effect of Bottom Contours

Because of the effect of the bottom, significant changes begin to occur when the waves enter water that is shallower than one-fourth the horizontal distance between adjacent crests, and the waves eventually "break" near the shore. The greatest changes in waves take place over irregular bottom contours. For example, over submarine canyons divergence occurs, wave crests are stretched laterally and their heights decrease. Over submarine ridges the converse is true (Fig. 1).

Final breaker height can be determined by constructing a refraction diagram as explained in "Refraction of Ocean Waves; A Process Linking Underwater Topography to Beach Erosion," by W. H. Munk and M. A. Traylor (*Journal of Geology*, Vol. 55, No. 1, 1947, pp. 1–26).

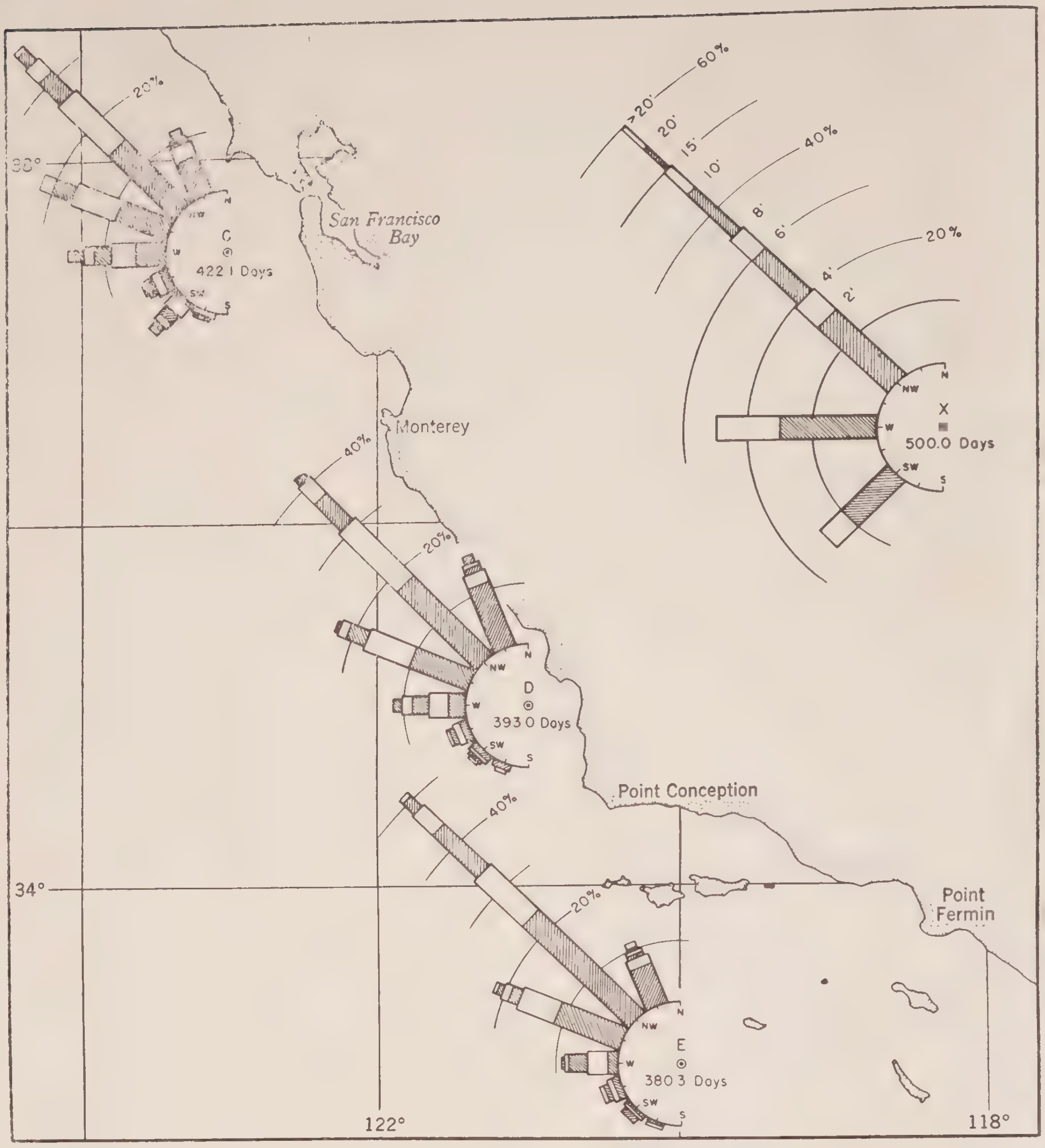

FIG. 2. DEEP-WATER WAVE HEIGHTS AND DIRECTIONS for winter months (December–March inclusive, 1936, 1937, 1938) are being used by Corps of Engineers in planning of shore and harbor protection structures on California coast. Diagram is from "A Statistical Study of Wave Conditions at Five Open Sea Localities Along California Coast, 1947," report prepared by Scripps Institution of Oceanography of University of California for Corps of Engineers, Los Angeles District.

Figure 1 is a simplification of a refraction diagram from Munk and Traylor for the area near the Scripps Institution of Oceanography for waves of 12-sec period from the WNW. The divergence over the submarine canyon off Sta. 1 is indicated by the spread of the orthogonals to the wave crests and results in waves breaking at 35 percent of the breaker height that would have occurred if there had been no refraction (refraction factor $K = 0.35$). The convergence over the submarine ridge off Sta. 2 results in waves breaking at 135 percent of their unrefracted breaker height ($K = 1.35$).

TABLE I. DATA FOR SAMPLE STATION X IN FIG. 2. TOTAL DAYS = 500

(1) Wave Height in Ft	(2) Percentage of Total Days When Wave Height Is Less Than Value in (1)				(3) Actual Number of Days When Wave Height Is Less Than Value in (1) (Percentage Times 500)			
	NW	W	SW	All Directions	NW	W	SW	All Directions
2	15	15	10	40	75	75	50	200
4	20	25	15	60	100	125	75	300
6	30			70	150			350
8	35			75	175			375
10	45			85	225			425
15	50			90	250			450
20	55			95	275			475
+20	60			100	300			500

NOTE: Directions NW, WNW, W, WSW, and SW include a range of 11¼ deg on each side. Direction NNW includes waves from 326¼ deg to 360 deg. Direction SSW includes waves from 180 deg to 213¾ deg.

Waves of the same average characteristics may extend over a large area in deep water off a coast. Thus, wave characteristics at several points on the shore can be obtained from the deep-water data at one point offshore using the theoretical graphs and refraction diagrams for each direction and period under consideration.

Computed Versus Observed Wave Data

There are three methods of obtaining wave data—visual observation, instrumental observation, and computation. Several years of almost continuous observations are necessary to give reliable mean and extreme wave conditions which may be expected at any point on a coast. For a given point, visual or instrumental observations would have to be taken over this entire period. The data obtained are generally valid only in the immediate vicinity so that both methods are expensive when data for a large number of localities are needed. Both methods fail to give accurately the direction from which the waves approach.

The computational method has the advantage of requiring only several months to compute data covering several years of time. Onshore data for many neighboring coastal locations may be obtained from the deep-water data at one point and the wave direction can be accurately computed.

Because visual observations vary considerably depending upon the experience of the observer, the computational method is more accurate. Computed data also compare favorably in accuracy with instrumental observations.

Applications

Many uses for computed data have been found. Munk in "Wave Action on Structures" (*Petroleum Technology*, December 1947) has made a study of the forces due to waves on objects such as piling. In the examples cited he computes the dimensions of the waves at the given locality by the hindcasting technique.

The hindcasting technique has been used at the Scripps Institution of Oceanography in two studies for the U.S. Navy and one for the U.S. Army. The Navy projects were statistical studies of wave conditions at certain open-sea localities and in given sheltered areas to aid in the design of seaplane hulls. The Army project was a study of wave conditions at five open-sea localities along the California coast. Similar studies may be made for any ocean area or for any natural or artificial lake for which wind data are available.

Data from the project undertaken for the Corps of Engineers, Los Angeles District, are being used by the Corps to aid in the planning of shore and harbor protection structures on the California coast. The Engineers are constructing refraction diagrams to determine the onshore wave characteristics from the deep-water data. Figure 2, based on data from the report on this project, shows the wave height and direction for winter months along the California coast. The frequencies of height and direction for waves of all periods are given by percent. If two or more wave trains appeared on the same day, each is accounted for in the frequency diagram. Thus, the total number of days upon which the percentages are computed varies from station to station and differs from the actual number of days in the given season. Going northward along the coast, the shift in predominant wave direction from northwest to west and the increase in percentage of larger waves reflects the northerly position of the storm tracks. However, the five stations at which computations were made, three of which are shown in Fig. 2, are located close enough to each other so that all coastal points are effectively accounted for.

From the wave energy distribution, the average work done by the waves as they pass a fixed line of given length parallel to the wave crests was also computed as a function of the wave period. This work may prove to be a useful quantity in the study of sand transport and wave erosion, inasmuch as the action on the sand in and near the breaker zone is closely related to the work expended.[1]

Two forecasters and three statistical clerks can compute, in about four months, the deep-water wave characteristics over a three-year period for the California coast. It is estimated that for an average station it would require about two months for one person to draw the necessary refraction diagrams and compute from the deep-water data the wave characteristics for a given coastal station.

A specific example will illustrate the application of the statistical wave data and refraction diagrams to an erosion problem. After construction of a breakwater on a short segment of the California coast occasionally subjected to high waves, most of the beach sand was moved into the lee of the structure by the action of waves and longshore currents. Subsequent attacks caused a recession of the beach and extensive property damage. This movement could have been predicted by using statistical wave data and refraction diagrams.

Refraction diagrams have shown that these exceptionally high waves are caused by strong convergence of the energy of wave trains from certain directions and with certain periods, as they move shoreward along the ridge at the edge of a submarine canyon. Statistical wave data confirm the actual observation that these critical waves occur relatively infrequently. In view of these facts, consideration is now being given to altering the original design of a proposed extension to the existing breakwater in order to enlarge the harbor and enclose the eroding area.

Conclusion

A speedy, accurate, and inexpensive method does exist for obtaining wave data. Data of this type are becoming increasingly important and are finding wider application in problems concerning beach and shoreline engineering.

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[1] "Littoral Transport on the California Coast," by R. O. Eaton, presented at Pacific Coast Meeting of American Geophysical Union, February 13–14, 1948, at Berkeley, Calif.

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Contribution No. 355

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REARING MARINE FISHES IN THE LABORATORY[1]

The rearing of marine fishes under experimental conditions has important applications in studies of speciation and evolution as well as in certain aspects of marine fisheries research. It seems appropriate, therefore, to describe methods which have resulted in the successful rearing of two marine species of the family Atherinidae, namely the grunion (*Leuresthes tenuis*) and the bay smelt (*Atherinops affinis littoralis*). These methods have been developed in the course of experiments designed to test the role of certain environmental factors in the determination of the number of vertebrae and of fin rays.

Under laboratory conditions the larvae of marine fishes have seldom been hatched and carried past the prolarval stage. The embryonic and early larval stages of a wide variety of marine species have been described from artificially reared material, but often the later stages have not been available, because, under laboratory conditions, the larvae have ordinarily died at the critical stage at which the yolk sac is absorbed and feeding begins.

Large-scale propagation of cod and other marine fishes has been carried out in both North America and Europe, but the practice has been to liberate the larvae in the sea shortly after hatching. Young plaice hatched in captivity have been held in outdoor ponds for several months (Herdman, Ann. Rep. Liverpool Mar. Biol. Comm., 1904, pp. 26-37). These ponds, however, had a standing crop of plankton organisms and additional feeding was not attempted. More recently it has been reported by Rollefsen (Cons. Perm. Int. Expl. Mer, Rapp. et Proc.-Verb., vol. 109, pt. 3, no. 26, 1939, p. 133) that plaice larvae have been reared by feeding with nauplii of the brine shrimp, *Artemia salina.* Our success also is largely due to the use of this food.

The procedure has been as follows. Eggs are fertilized by the dry method, well mixed, and allowed to stand for about one minute. The excess milt is then washed off and the eggs are placed in beakers containing a liter of sea water, in which they sink to the bottom. Percentage mortality is increased if more than a single layer of eggs covers the bottom of the container. Aeration is provided and the stream of air adjusted so that the eggs do not circulate. Successful incubation is also obtained in trays of mosquito netting suspended in running-water aquaria.

On hatching, the prolarvae are transferred to previously prepared five-gallon aquaria of aerated standing sea water containing an adequate crop of plankton. To hasten the plankton production a culture of microorganisms may be introduced from a stock tank. Nets should not be used in handling the early stages, which should be transferred to the tanks directly by pouring, or by means of a suitable dip-tube.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 355.

For a food supply, brine shrimp are cultured from dried eggs in jars of aerated sea water.[2] The freshly-hatched nauplii are introduced into the tanks well before the yolk sac of the fish is absorbed. Grunion and bay smelt prolarvae begin feeding when about two days old, while still provided with a yolk sac, although they will live for several days without feeding. Nauplii are added daily in quantities sufficient to maintain a moderate excess.

Best results have been obtained by allowing the water to stand unchanged so that a considerable growth of attached filamentous green algae develops. Larvae have also been reared in running water, but more than half of these developed abnormalities such as crooked bodies and open mouths, perhaps because of nutritional deficiencies. Most of the young fish thus reared were preserved at the end of 30 days since they were sufficiently far advanced for the purpose of the experiments. At this time all the vertebrae were ossified and usually the fin rays and some of the scales were formed. Some fish, however, have been held for longer periods. At the time of writing one sample is in its fourth month of life.

To date it has not been possible to obtain normal growth or completely balanced development. For example, growth in length is apparently slower than it is in nature, although ossification may progress at almost the same rate. It is hoped that through improved technique normal development can be approximated in aquaria. The method could then be applied to a very wide range of investigations.

The authors wish to thank Dr. Carl L. Hubbs for his interest and advice during the course of the work.—*J. L. McHugh and Boyd W. Walker, Scripps Institution of Oceanography, La Jolla, California,* August, 1947.

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[2] Brine shrimp eggs, from salt works on San Francisco Bay, were kindly supplied by Dr. Wilbert M. Chapman of the California Academy of Sciences. Such eggs are sold by the San Francisco Aquarium Society, Golden Gate Park, San Francisco.

Contribution No. 356

RELATION OF SALINITY TO THE ACTIVITY OF THE SPERMATOZOA OF *GILLICHTHYS*, A MARINE TELEOST

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RELATION OF SALINITY TO THE ACTIVITY OF THE SPERMATOZOA OF *GILLICHTHYS*, A MARINE TELEOST[1]

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THE purpose of this experiment is to analyze the effects of salinity on the activity of the spermatozoa of the long-jawed goby or mudsucker, *Gillichthys mirabilis*. Since this teleost is a marine species, its spermatozoa are subjected to an entirely different environment than are those of the salmon and trout, which spawn in fresh water. The latter are the fishes that have been chiefly used in determining the relation of osmotic pressure to the period of activity of the spermatozoa.

The activity of trout spermatozoa in river water is very brief (Gray, 1920). Since NaCl and Ringer solutions, as well as diluted sea water, prolong the activity of trout spermatozoa, Huxley (1930) suggests that the trout, though somatically adapted to fresh water, is imperfectly adapted to reproduction in that medium. Ellis and Jones (1939) believe the effects to be osmotic rather than ionic because salmon spermatozoa live for about the same length of time in solutions of either sucrose or sea water which have the same osmotic pressure. These authors think that the spermatozoa are not so ill adapted to their environment as Huxley indicates. Fluid from salmon eggs greatly lengthens the life of the spermatozoa. The spermatozoa must endure only a short contact with fresh water before they enter the more advantageous medium of the egg fluid.

MATERIALS AND METHODS

Filtered sea water was prepared in stock solutions ranging from 10 to 200 per cent concentration. The sea water was diluted with glass-distilled water. Concentrations above 100 per cent were obtained by evaporation. Artificial sea water was made according to the formula proposed by Brujewicz (Sverdrup, Johnson, and Fleming, 1946, p. 186). This was diluted or concentrated to solutions of osmotic pressure similar to the sea-water solutions. Corresponding osmotic solutions were also prepared with glucose in distilled water and with sucrose to which $CaCl_2$ had been added. The pH of all solutions was determined with a Coleman glass electrode.

The gobies were taken during their period of greatest spawning activity, March–May (Weisel, 1947). The testes were removed from freshly killed fish, and equal portions were placed in watch glasses containing the solutions of different osmotic pressure. Testes from the same fish were used in each series of dilutions, and two to four series were run for each different solute tested. A large drop of the solution was put on a clean cover slip, and the piece of testis was immediately teased apart in the drop. A hanging-drop preparation was then made—well sealed with vaseline. The preparations were examined under the microscope. A record was kept of the time at which all movement of the spermatozoa ceased. Other measurements for the termination of the experiments were und to be less uniform and subject to servational fallacies.

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[1] Contributions from Scripps Institution of Oceanography, New Series, No. 356. I am indebted to Dr. Frederick Crescitelli for helpful suggestions and to Dr. Carl L. Hubbs for revising the manuscript.

This procedure was used because it is fficult to strip milt from this fish. The stes are very small. The diameter rare- exceeds 2.00 mm., even during the awning season. Also, the contents of e relatively large seminal vesicle are ixed with the spermatozoa if the fish is ripped. Since the vesicular fluid con- ins salts and a large amount of oteoses (Young and Fox, 1937), it was nsidered that this fluid would alter the motic pressure of the solutions more an teasing a small portion of testis in e respective solutions.

EXPERIMENTAL RESULTS

I. ACTIVITY IN SEA WATER

To determine the lowest salinity at hich the spermatozoa become active, a-water solutions were diluted in grades 1 per cent from 10 to 40 per cent. Ac- vity first commenced at 17 per cent. eble movements were exhibited in utions of 17–24 per cent. In all higher ncentrations practically all sperma- zoa were activated. However, activa- n was effected less rapidly in 25 per nt sea water than in the higher concen- tions. In 25 per cent solution, 2–5 nutes were required to produce motili- over the entire field, but, once ac- ated, the spermatozoa displayed the me rapid motion as in the solutions of reater pressure.

Stock solutions ranging from 18 to 200 er cent were tested with spermatozoa om four fish. The spermatozoa of each sh survived longest in 25 per cent sea ater. Figure 1 indicates the shortening survival time from this optimum as e concentrations become greater or less. he curve falls much more rapidly in ncentrations below 25 per cent than it oes in those above. Spermatozoa from the different fish differed in absolute survival time, but the relative survival times were similar.

II. ACTIVITY IN ARTIFICIAL SEA WATER

In artificial sea water (Fig. 1) the spermatozoa behaved about the same as they did in true sea water. The spermatozoa showed first signs of motility at a concentration of 15 per cent artificial sea water. In one sample they lived as long in 20 as they did in 25 per cent concentration. These were minor discrepancies. The artificial sea water was used to avoid the rather large and irregular variations in pH. In the true sea-water concentrations ranging from 15 to 200 per cent, the pH varied as follows: 7.8, 7.8, 8.0, 8.0, 7.8, 9.1, 8.9, 8.5. In the artificial sea-water concentrations grading from 15 to 150 per cent, the values were: 8.4, 8.0, 7.95, 7.9, 7.95, 8.3.

Spermatozoa which had been inactivated in 10 per cent artificial sea water became active when the solution was brought to a higher concentration. Those which had been in fresh aquarium or distilled water for a few minutes, however, showed no signs of motility when the water was brought to a concentration as high as 100 per cent osmotic pressure of sea water. Spermatozoa which in time had become inactive in 150 per cent artificial sea water were not reactivated by dilution.

III. ACTIVITY IN NONELECTROLYTES

In an effort to determine whether the observed differences in spermatozoan activity at different salinities were due to the effects of the particular ions in sea water or merely to the osmotic pressure, solutions of glucose with the same osmotic pressure as those of the sea water were tested. The spermatozoa were not activated below concentrations of 50 per cent. At this concentration the spermatozoa were motile for a longer period than in higher concentrations (Fig. 2). It seemed likely that in glucose, as compared with sea water, there was a difference in permeability. In an attempt to provide a medium to which the cells were less permeable, solutions of sucrose were made with $CaCl_2$ added. Here again the optimum solution was at 50 per cent of the osmotic pressure of sea water (Fig. 2). In one trial the spermatozoa were motile in a solution as low as 20 per cent. In the solutions of both sugars the results were not so uniform as in the artificial and true sea waters. Furthermore, the activity was less protracted.

IV. EFFECT OF pH

A few tests were undertaken to check the possibility that differences in pH may have affected the results recorded above. Solutions of 50 per cent artificial sea water were titrated with HCl or NaOH to a pH of 4.8, 6.05, 7.1, 7.55, 8.25, 9.25, and 10.15. The extremes of this series well exceeded the pH of any of the solutions tested in the previous experiments. There was no noticeable difference of

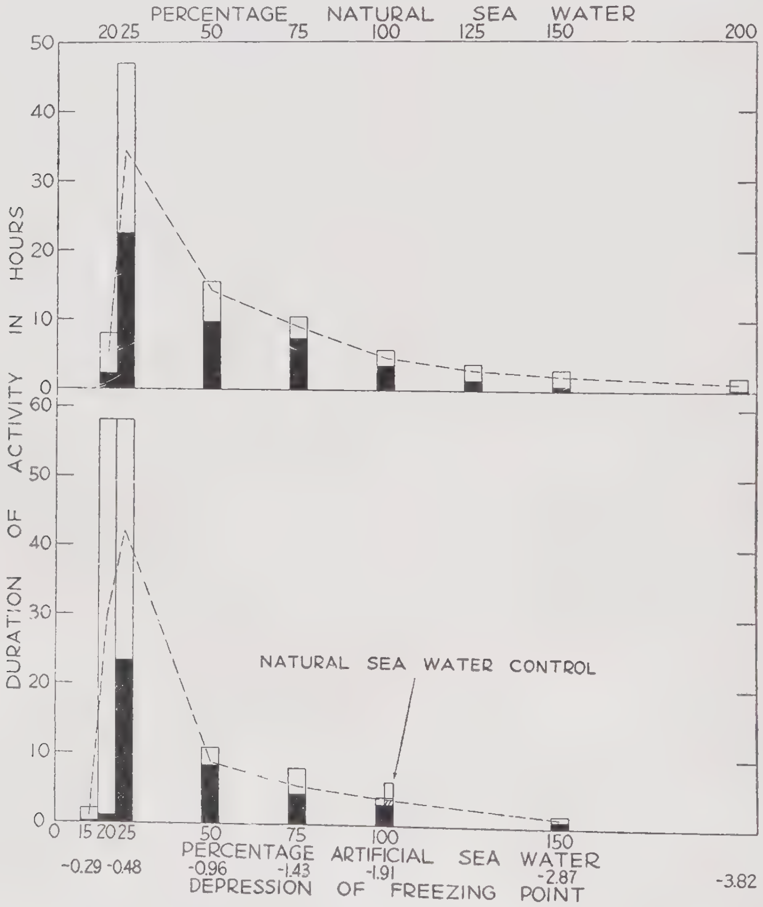

FIG. 1.—Survival of goby spermatozoa in different concentrations of true and artificial sea water. Total height of column equals maximum survival time in four experiments, two slides for each experiment. Height of dark area equals minimal survival time. The curve is plotted on points which are average survival times for the different trials in each solution. Temperature 23°–26° C.

ehavior of the spermatozoa in the dif rent pH concentrations. They all be ame inactive at practically the same me.

V. PROLONGATION OF ACTIVITY AT LOW TEMPERATURE

Temperature, on the other hand, had remarkable effect on the period of spermatozoan motility. The spermatozoa from one fish were placed in the various concentrations of artificial sea water. One set of the slides was kept in a refrigerator at a temperature of 2°–4° C. A similar set from the same testes was retained at room temperature, 24°–26° C. The spermatozoa in 17 per cent solution became inactive at the same time; but in all the higher concentrations the spermatozoa lived for a much greater length of time at the lower temperature (Fig. 3). Those in 20 and 25 per cent showed activity for over 2 weeks as compared to 33 hours for those kept at room temperature in the same solutions. It is presumed that they were in motion throughout this long period, for they showed activity when the slide was placed under the microscope immediately after removal from the refrigerator.

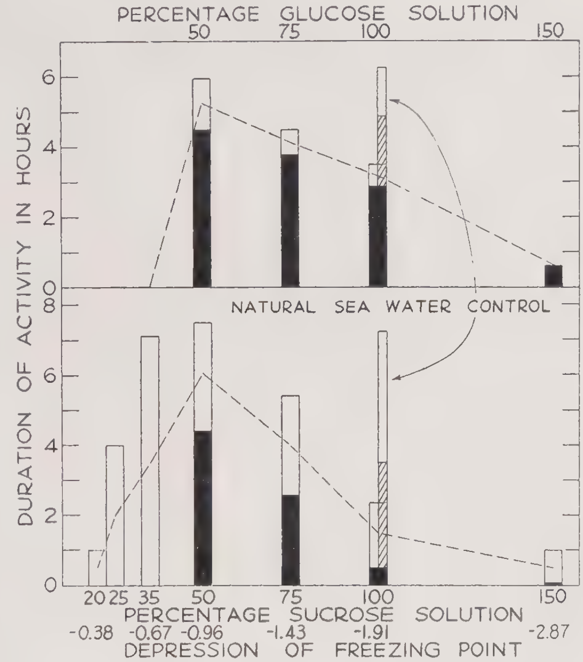

FIG. 2.—Survival of goby spermatozoa in glucose and sucrose solutions osmotically equivalent to the a-water solutions. $CaCl_2$ added to the sucrose. Total height of column equals maximum survival time in vo experiments, two slides for each experiment. Height of dark column equals minimal survival time. emperature 24°–26° C.

VI. RELATION OF "SEMINAL VESICLE" TO ACTIVITY OF SPERMATOZOA

The gobies are among the few teleosts that possess a well-defined "seminal vesicle." Some attention was given to the possible relations of the "seminal vesicle" to the duration of activity of the spermatozoa of *Gillichthys*, since Eggert (1931) claimed that the fluid extracted from the vesicles of a related species, *Gobius panizzae*, seemed to prolong the life of the sperm. Neither in origin nor in structure is this organ closely similar to the seminal vesicle of mammals. It is primarily a secretory organ (unpublished personal observations), but its physiological function has not been determined.

That no prolongation of spermatozoan activity can be attributed to the vesicular extracts of *Gillichthys* was indicated by Young and Fox (1937) and is confirmed by the present study. Twelve slides were prepared, six with spermatozoa in a drop of sea water alone and six with the spermatozoa in a drop to which vesicular fluid had been added. The movements on each slide ceased within a few minutes of one another. There was no significant difference in the length of activity.

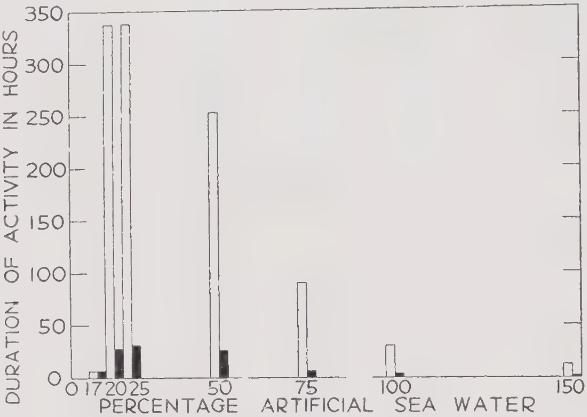

FIG. 3.—Survival of goby spermatozoa in different concentrations of artificial sea water and at different temperatures. Height of light column equals survival time at 2°–4° C. Height of dark column equals survival time at 24°–26° C. A control in 100 per cent true sea water reacted similarly to that in the 100 per cent artificial sea water.

Vesicular fluid was also tried with lower concentrations of sea water. No visible prolongation of the life of the spermatozoa could be noticed, nor were they active below concentrations of 18 per cent. Observations were not continued to the termination of the experiments at all the dilutions. It was considered that any differences observed could have been caused by the changes in osmotic pressure that resulted from the addition of the vesicular fluid.

VII. MISCELLANEOUS OBSERVATIONS

The fish used in all these tests were kept without food, some for as long as 4 weeks. Inanition had no effect on the motility of the spermatozoa, nor did it reduce the period of activity.

Three gobies were placed in fresh water for 2 weeks before their testes were removed. Spermatozoa from these fish were active in 100 per cent sea water but were inactive in 10 per cent (the only dilution tested).

DISCUSSION

The methods used in the experiments did not lead to very precise determinations. With the addition of spermatozoa to the solutions, there was an unavoidable addition of materials which must have changed the osmotic pressure from that calculated. The gaps between the percentages of the solutions tested did not permit the determination of an exact optimal percentage. Since the teased spermatozoan preparations contained ions, the sugar solutions were not truly nonelectrolytic after the spermatozoa had been introduced. Also the number of spermatozoa in each preparation varied.

Since low temperatures markedly proonged the life of the spermatozoa, no doubt the failure to control the temperature closely in the exeriments introduced an error. This error was probably not large, however, for the temperature differences were limited and all the experiments were subjected to approximately the same fluctuations (see explanation of figures).

Within the wide limits between which they were tested, the spermatozoa do not appear affected by the pH concentrations. For this reason it may be assumed that no serious error was introduced because of the fact that the pH value varied in the different solutions. Young and Fox (1937) found the pH of unbuffered sea water to drop from 8.1 to about 6.3 during the progress of similar experiments. They state that buffering the sea water and placing N/10 KOH in the slide well to absorb the CO_2 generated did not affect the length of life of the spermatozoa.

Attempts to determine the degree of activity in the various solutions and to correlate this with the length of life were unsuccessful. The movements were obviously reduced in the solutions of minimum osmotic pressure. However, it was in these solutions that the time of motility was shortest. In all the solutions of higher pressures the spermatozoa seemed to have equal activity.

In spite of these limitations, I believe the experiments allow one to arrive at certain generalizations.

The spermatozoa of the long-jawed goby are active over a surprising range of osmotic pressure. If the delta of the sea water is taken as $-1^\circ.91$, this range extends from $\Delta = -3^\circ.82$ to $\Delta = -0^\circ.33$. To my knowledge, no other teleost spermatozoa investigated are active over such a wide range. This wide tolerance is possibly connected with the life-habits of *Gillichthys*. The fish themselves are capable of living for some weeks both in fresh water and in supersaturated sea water (personal observations). It is also likely that they spawn in sea water of different concentrations.

At $\Delta = -0^\circ.48$ (25 per cent) sea water and artificial sea water, the spermatozoa live for a much longer time than at pressures above or below this. However, in nonelectrolytic solutions the longevity is greatest around $\Delta = -0^\circ.96$ (50 per cent).

It would naturally be assumed that the spermatozoa live longest in solutions isotonic with the fish body fluids. In all probability they are in osmotic equilibrium with the blood of the fish. Davson and Danielli (1943) find the eggs of salmon and trout to have the same osmotic pressure as the female's blood, and Krogh (1939) states the same to be true for two marine teleosts.

The blood of marine fishes has a definitely higher osmotic pressure than that of fresh-water fishes and of anadromous forms in fresh water. The average for seventeen different salt-water species is $\Delta = -0^\circ.84$, whereas the average for six fresh-water fish is $\Delta = -0^\circ.54$ (tables from Mathews, 1920; Davson and Danielli, 1943; and Heilbrunn, 1943). When taken on their fresh-water spawning grounds, the serum of the male Pacific salmon has a mean of $-0^\circ.668$ and the ovarian fluid of $-0^\circ.559$ (Greene, 1904).

It is apparent that the blood of marine teleosts has a much higher osmotic pressure than do the dilutions of sea water, true and artificial, in which the goby spermatozoa live the longest. The reaction of the spermatozoa in the nonelectrolytic solutions more nearly parallels what might be expected. The sugar solution which provides the maximum period of activity has a pressure of $\Delta = -0^\circ.96$. This is much closer to osmotic equilibrium with the blood of the fish (Table 1).

Although the salmon (*Salmo salar*) spends most of its adult life in the ocean, it develops in fresh water, and it migrates to fresh water to spawn. Its spermatozoa live a much longer time in dilutions of sea water than they do in river water. The duration of activity is greatest in sea water diluted to Δ = −0°.38 (20 per cent). In sucrose solutions the activity is longest in a solution of Δ = −0°.48 (25 per cent of sea water) (Ellis and Jones, 1939). These are both somewhat lower than the probable osmotic pressure of the blood. As in the goby, the optimum sugar solution has a higher pressure than the optimum sea-water dilution. The difference, however, is much less.

The osmotic pressure of a solution in relation to a membrane is not dependent wholly on the concentration of the solution. The pressure decreases in proportion to the ease with which the substances pass through the membrane. That there is a difference for the optimum concentrations of sea water as compared with sugar solutions indicates that we are here dealing with such a condition. It is possible that there is an outward penetration of substances from the spermatozoa in isosmotic solutions of sea water. Solutions of sea water in which spermatozoa survive longest have a markedly lower osmotic pressure than does the blood of the fish. Optimum sugar solutions are more nearly isosmotic.

Ellis and Jones (1939) believe that the activating effect of sea water is osmotic rather than ionic. Their salmon spermatozoa lived slightly longer in sea-water dilutions than they did in sugar solutions; but Ellis and Jones did not believe that they had undertaken enough experiments to make the finding significant. In all my investigations the goby spermatozoa lived much longer in the sea water, true and artificial, than in either of the sugars. Though the osmotic factor is a major one, my data indicate that the ions also play an important role. The sea-water dilutions are a better medium for the spermatozoa than are osmotically identical sugar solutions.

The spermatozoa of the salmon and the long-jawed goby are longest active at nearly the same concentration of diluted sea water. The same is probably true also of the spermatozoa of the trout (in his short note, Huxley [1930] states that trout spermatozoa lived longest in sea water diluted to 25 per cent with tap water). Yet this goby spawns in sea water or in somewhat diluted sea water, whereas the salmon spawns in fresh water. There is, however, a marked adaptation in both cases to the environment in which they spawn. The salmon spermatozoa are active, though for a short time, in fresh water and are inactive in concentrations above 40 per cent sea water. The goby spermatozoa are totally inactive in fresh water, become active at about 17 per cent sea water, and maintain motility even in supersaturated sea water. The spermatozoa of the goby are much better

TABLE 1

RELATION OF OSMOTIC PRESSURE OF THE BLOOD TO SOLUTIONS OPTIMUM FOR SPERMATOZOAN ACTIVITY

Approximate Osmotic Pressure of Blood		Osmotic Pressure of Solution for Optimum Activity of Spermatozoa	
Salmon (fresh water)	Δ = −0°.60	Sucrose	Δ = −0°.48
		Sea water	Δ = −0°.38
Goby (salt water)	Δ = −0°.84	Sucrose and glucose	Δ = −0°.96
		Sea water	Δ = −0°.48

dapted to their natural medium than are those of the salmon. The fact that the bays and estuaries inhabited by *Gillichthys* are subject to an influx of fresh water during the period when this goby spawns may be related to the fact that the spermatozoa are longest active at a reduced salinity. Determinations for other species, however, are needed to verify this possibility. It would be interesting to make comparisons with fishes that are permanently resident in fresh water and with oceanic fish that are not estuarine dwellers.

For the survival of the species, there would probably be no added advantage for the goby spermatozoa to live a longer time than they do in their natural spawning medium. The spermatozoa can live at least 3 hours in sea water at usual temperatures. In this time they must certainly be capable of fertilizing the eggs. The goby males and females spawn practically simultaneously and in close proximity (Weisel, 1947). Since the spermatozoa become active more quickly in straight sea water, it is actually more advantageous for the spawning to occur in this medium rather than in the solution for optimum survival time. The lag of [illegible]–5 minutes in activation of the spermatozoa in 25 per cent sea water might lead to failure in fertilization.

Obviously, the fluid from the "seminal vesicle" aids little, if any, in propagation of the species by prolonging the life of the spermatozoa as some have suggested. Its function is obscure.

Unlike the trout (Huxley, 1930), the long-jawed goby is adapted to its normal environment not only somatically but also for reproduction.

There appears to be no adaptational significance and perhaps no historical significance to the ability of the *Gillichthys* spermatozoa to remain active for many days at low temperature. This ability may merely reflect the general rule that low temperatures retard the rate of biological processes.

SUMMARY

1. The spermatozoa of the long-jawed goby are active over a wide range of osmotic pressure—from 17 to 200 per cent sea water. They are motile longest in 25 per cent sea water and in glucose and sucrose solutions that have the same osmotic pressure as 50 per cent sea water. The optimum activity in 25 per cent sea water may be related to the fact that the salinity in the goby's habitat is often reduced during the spawning season.

2. The concentration of true and of artificial sea water at which the spermatozoa live longest is not isosmotic to the spermatozoa. Optimum sugar solutions are more nearly isosmotic.

3. The spermatozoa live longer in various concentrations of sea water than in osmotically equivalent sugar solutions. Though the activating influence of the sea water may be largely osmotic, the ions also appear to play an important role.

4. A lower temperature markedly prolongs the life of the spermatozoa in the different concentrations of artificial sea water. In 25 per cent concentration at 2°–4° C. the spermatozoa remained alive for 2 weeks, whereas controls at 24°–26° were immobile in 33 hours. The prolonged activity of the spermatozoa at low temperatures probably has no adaptive significance.

5. Fluid from the goby's "seminal vesicle" does not prolong the life of the spermatozoa. The function of the vesicle remains obscure.

6. The spermatozoa of the fresh-water-spawning salmon and the salt-water-spawning goby survive longest in sea-water dilutions of about the same osmotic pressure. In spite of this similarity

the activity of the spermatozoa appears to differ in correlation with their respective environments. The spermatozoa of the goby are inactive in fresh water but are active in undiluted sea water, whereas those of the salmon are active in fresh water but are inactive in normal sea water.

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Fatty Acid Transformations by Anaerobic Bacteria [1]

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University of California, La Jolla

Received August 4, 1947

INTRODUCTION

There is little factual information relating to the means by which fatty acids are transformed anaerobically in nature. The bacterial consumption or alteration of many fatty acids has been observed repeatedly under aerobic conditions. Acids involved have varied considerably in chain length and have included both saturated and unsaturated types (2, 4, 6, 10, 11, 12, 13, 15, 20). The rates of aerobic change fluctuate among species and substrates, but Peppler (17) has reported certain fatty acids to be more readily oxidized than glycerol by *Pseudomonas aeruginosa.*

The claim that fatty acids are not subject to decomposition by anaerobic bacteria (19) has been successfully challenged by several investigators. Clarke and Mazur (5) found that the rate of disappearance of fatty acids from diatoms and marine muds was greater under nitrogen than in an aerobic environment. The range of fatty acids consumed anaerobically is apparently as great as that attacked under aerobic conditions (27). The anaerobic nature of the bacteria involved is indisputable, for included are the genera *Clostridium* and *Desulfovibrio* (1, 7, 16, 18).

Anaerobic oxidation of fatty acids has been observed. Stone *et al.* (25, 26) noted that various species of *Propionibacterium* activated formic, acetic, and propionic acids as hydrogen donors. In these reactions methylene blue, nitrates, or *o*-chlorophenolindophenol functioned as hydrogen acceptors. Formic acid also served as an oxidant in a few instances. The dehydrogenation of formic acid has been activated also by anaerobic lipoclasts (21). Peculiarities in the behavior of formic acid have tended to exclude it from classification as a fatty acid. Nevertheless, its importance in the anaerobic changes affecting fatty acids is sufficiently great to warrant its inclusion in any such study.

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Some type of dehydrogenation may account for the observations of Reynolds and Hopkins (20), who reported increases in the iodine number of oleic acid subjected to bacterial attack. However, the desaturating effect was greater under aerobic than anaerobic conditions.

In some cases bacteria have induced hydrogenation and, possibly, other types of fatty acid reduction. One such reducing influence is that affecting unsaturated acids. Schönbrunner (23) repeatedly observed saturation of oleic and sorbic acids by various soil and mud samples as well as by several pure bacterial cultures. The acids were saturated to more than 60% of completion. Saturation of lipides by bacteria in an anaerobic environment also is reported by Ginsburg-Karagicheva and associates (8, 9).

Bacteria are likewise known to reduce saturated acids. Prominent among these compounds are the volatile fatty acids important as fermentation intermediates. The data of Blanchard and MacDonald (3), Mickelson and Werkman (14), and Severson (24) illustrate the reduction of propionic and butyric acids to their corresponding alcohols. The conversions evidently represent a direct reduction of the carboxyl group, for isomeric configurations were preserved in the transition from fatty acid to alcohol. Severson (24) showed that the transformation product of acetic acid was almost entirely acetone, which also represented a partial reduction product of propionic and butyric acids. It is significant that the production of gaseous hydrogen during fermentation was depressed as acetic and propionic acids were reduced (14). This demonstration provokes speculation concerning the possible activation of hydrogen and its consumption as an agent in the reduction of the carboxyl group.

The bacterial reduction of saturated fatty acids is not confined to water-soluble compounds. ZoBell (31) has described the alteration of capric acid under the influence of a mixed culture containing the strongly anaerobic sulfate-reducing bacteria. This culture produced an oil-like, ether-soluble, unsaponifiable material. Determinations of refractive index, birefringence, and optical activity tended to classify the material as a normal paraffin. Most of the crystals appeared to be $C_{22}H_{46}$, or in the range from C_{20} to C_{25}. The behavior of the crystals when heated was similar to that of the petroleum ceresins. The mechanism of the transformation was not determined and may have included decarboxylation and polymerization reactions. There have been several other reports of the bacterial reduction of fatty acids to petroleum hydrocarbons, but few of them are more than unsubstantiated speculations.

These isolated descriptions of the bacterial utilization of fatty acids coupled with the demonstration of lipide hydrolyses by anaerobic bacteria (22) have emphasized the importance of tracing the further transformation or degradation of the liberated fatty acids. The following data may be of some aid in this endeavor.

TRANSFORMATION OF FATTY ACIDS BURIED IN MARINE SEDIMENTS

Examination of marine sediments affords proof of the anaerobic changes affecting naturally occurring fatty acids. Results given in

Table I describe lipide fractions of marine mud core SL601 and represent an average of duplicate determinations.

TABLE I

Vertical Distribution of Lipides in Marine Sediments

Lipide material	Core level in inches 14–20	 40–48
Estimated age, in years	210–300	600–720
Unsaponifiable material, per cent by dry weight	0.0115	0.0076
Fatty acids, per cent by dry weight	0.0085	0.0052
Molecular weight	355	383
Iodine number	52	26

Two levels of the core were dried at 70°C., powdered, and extracted in a Soxhlet apparatus with alcohol-ether (3:1). The crude extract was fractionated according to the gravimetric procedure of Wilson and Hansen (29), and the iodine numbers were determined by the method of Yasuda (30).

Quantitative distribution of the lipides is not susceptible to exact interpretation. The amounts recovered depend upon several factors, including stratification at deposition and bacterial consumption or production. However, the characteristics of the extracted fatty acids are of more interest. Increases, with geologic age, in acid chain-length can perhaps be accounted for on a basis of preferential consumption of shorter molecules and the possible bacterial alteration of existing compounds. Similar reasoning may be applied to the saturation of fatty acids with depth. The possibility that stratification was responsible for these important differences in the degrees of saturation was minimized by studies on additional material. Analyses are summarized in Table II.

TABLE II

Saturation Gradient of Fatty Acids in Marine Sediments

Lipide material	Core level in inches					
	0–8	8–18	18–24	30–36	36–40	40–44
Estimated age, in years	0–80	80–180	180–240	300–360	360–400	400–440
Fatty acids,						
Per cent by dry weight	0.0179	0.0241	0.0110	0.0143	0.0306	0.0139
Iodine number	45	50	33	35	30	27

Determinations were similar to those described above, except that the core sections were dried under conditions which minimized autooxidation of labile material. Immediately upon collection at sea, the core (XXIX:149–102) was sectioned and placed in glass jars, each of which was then completely filled with sea water and sealed. Oxygen dissolved in the water was reduced quite rapidly, for a pronounced odor of hydrogen sulfide was noted when the jars were opened for subsequent treatment. Within 3 hours of collection the muds were transferred to acetone, sealed, and stored at room temperature for 24 hours. Then followed similar treatment with several charges of absolute ethyl alcohol. Desiccation was completed by *in vacuo* treatment over Drierite at room temperature. The acetone-alcohol filtrates were pooled and combined with subsequent alcohol-ether extracts. These combinations were reduced in volume by vacuum distillation prior to fractionation.

The quantitative distribution of fatty acids again appears to be without significance, but the changes in iodine number are important. Although exceptions to a smooth curve are evident, there is ample evidence of a general saturation with increasing age of the acid.

The data do not indicate whether the saturations were the result of a preferential consumption of unsaturated fatty acids, a reduction at double bonds, or a combination of both factors. Further, the changes in the fatty acid content of sediments are not in themselves direct evidence for the activity of anaerobes, although they strongly suggest the functioning of bacterial agents. Determination of the motivation for these, and other, changes in naturally occurring fatty acids prompted more direct studies into the effects of anaerobic bacteria upon such compounds.

Growth of Anaerobes upon Fatty Acids

Both facultative and obligate anaerobes are known to hydrolyze lipides in anaerobic environments. The two types of bacteria were, therefore, tested for their abilities to utilize fatty acids as sources of carbon and energy. Table III depicts the results observed.

Cultures were prepared in glass-stoppered bottles, employing the mineral salts solution and techniques described previously (22). Fatty acids were added as potassium salts and in amounts sufficient to give a final concentration of 0.05%. Inocula were obtained from several types of mud and water samples which harbored large numbers of facultative and obligate anaerobes capable of lipid hydrolysis. Duplicate series of cultures were included and contained 0.05% of glycerol in addition to the fatty acids as a check upon inoculum viability and fatty acid toxicity. Cultures were examined for growth during incubation for 34 days at 27°C.

Culture CS-1, the only inoculum to develop consistently upon fatty acids without glycerol, was able to utilize both saturated and unsaturated acids. Its failure to grow upon caprylic and pelargonic

TABLE III

Growth of Anaerobes on Fatty Acids and on Fatty Acid-Glycerol Combinations During Incubation for 34 Days at 27°C.

Substrate	Growth of inoculum.					
	D-1	PE-2	CS-1	SS-1	SL496-1	M-1
Mineral salts solution	−	−	−	−	−	−
Glycerol	+	+	+	+	+	+
Saturated:						
Formic acid	−	−	+	+	−	−
Formic acid + glycerol	−	−	+	+	−	−
Acetic acid	−	−	+	−	−	−
Acetic acid + glycerol	−	−	+	+	−	−
Propionic acid	−	−	+	−	−	−
Propionic acid + glycerol	−	−	+	−	−	−
Butyric acid	−	−	+	−	−	−
Butyric acid + glycerol	−	−	+	−	−	−
Valeric acid	−	−	+	−	−	−
Valeric acid + glycerol	−	−	+	−	−	−
Caproic acid	−	−	+	−	−	−
Caproic acid + glycerol	−	−	+	−	−	−
Enanthic acid	−	−	+	−	−	−
Enanthic acid + glycerol	−	−	+	−	−	−
Caprylic acid	−	−	−	−	−	−
Caprylic acid + glycerol	−	−	+	−	−	−
Pelargonic acid	−	−	−	−	−	−
Pelargonic acid + glycerol	−	−	−	−	−	−
Capric acid	−	−	+	−	−	−
Capric acid + glycerol	−	−	+	−	−	−
Lauric acid	−	−	+	−	−	−
Lauric acid + glycerol	−	−	+	−	−	−
Myristic acid	−	−	+	−	−	−
Myristic acid + glycerol	−	−	+	−	−	−
Palmitic acid	−	−	+	−	−	−
Palmitic acid + glycerol	−	−	+	−	−	−
Stearic acid	−	−	−	−	−	−
Stearic acid + glycerol	−	−	+	−	−	−
Unsaturated:						
Undecylenic acid	−	−	+	−	−	−
Undecylenic acid + glycerol	−	−	+	+	−	−
Oleic acid	−	−	+	−	−	−
Oleic acid + glycerol	−	−	+	+	−	−

acids is probably attributable to the toxicity of their soluble salts. Potassium stearate was converted to highly insoluble calcium and magnesium salts apparently incapable of supporting growth. It should be noted that only inoculum CS-1 produced a sulfate-reducing culture which, of course, was obligately anaerobic. Fatty acids failed to support the growth of facultative cultures, proved to be viable by their development upon glycerol. This circumstance may be related to the lack of a reducible substance, although growth failure upon combinations of acids and glycerol suggests that substrate toxicity was paramount.

A large group of mixed cultures, each containing sulfate-reducing anaerobes, was next tested upon a series of fatty acids added as potassium salts in the manner described above. The cultures were examined during a period of 30 days for evidence of sulfide production and, thus, fatty acid oxidation. The distribution of fatty acid-oxidizing cultures is noted in Table IV.

TABLE IV

Growth of Sulfate-Reducing Cultures on Fatty Acids During Incubation for 30 Days at 27°C.

Acid	Cultures tested	Cultures which developed
Acetic	62	14
Propionic	62	4
Butyric	62	4
Valeric	62	3
Caproic	62	3
Enanthic	62	3
Caprylic	62	1
Pelargonic	62	3
Capric	62	3
Lauric	62	4
Myristic	62	4

The ability of sulfate reducers to oxidize fatty acids appears to be limited by two factors, toxicity and solubility of substrate. The cultures were tested in a sea-water medium, and a considerable portion of the substrate was precipitated in the form of calcium and magnesium salts. The precipitation was most pronounced with acids above the caprylic level. Thus, while the inhibitory powers of myristate for sulfate reducers may be greater than those of caprylate, the greater solubility of the latter results in more pronounced toxic effects.

Fatty Acid Dehydrogenations

The indicated ability of sulfate reducers to oxidize a variety of fatty acids, and the failure of non-sulfate-reducing anaerobes to do so, led to an investigation of these behaviors by other than cultural means.

Cultures were purified prior to enzymatic studies. The incidence of fatty acid dehydrogenations is described in Table V.

TABLE V

Dehydrogenation of Fatty Acids by Anaerobic Bacteria

Acid	Non-sulfate reducers		Sulfate reducers	
	Tested	Active	Tested	Active
Saturated:				
Formic	7	7	5	2
Acetic	7	1	5	2
Propionic	7	1	5	0
Butyric	7	3	5	2
Valeric	7	2	5	1
Caproic	7	2	5	1
Enanthic	7	1	5	0
Caprylic	6	0	5	1
Capric	6	0	5	0
Lauric	6	1	5	0
Myristic	6	0	5	0
Palmitic	6	1	5	1
Stearic	6	2	5	4
Unsaturated:				
Undecylenic	6	0	5	0
Oleic	6	1	5	1
Linoleic	5	3	5	2
Linolenic	5	3	5	2

Cells were prepared by growing non-sulfate-reducing cultures in 5-gal. bottles filled with a mineral salts solution supplemented by 1.0% of Bacto peptone, 0.3% of yeast extract, and 0.02% of ascorbic acid. The filled and inoculated bottles were fitted aseptically with a sterile rubber stopper carrying a mercury check-valve, although free gases were not generally produced. The growth period was 24–48 hours at 27°C. Sulfate reducers were cultivated similarly, except that 1.0% of glucose was added. Cultures were incubated for 48–72 hours at 27°C. Cells were recovered by passage of the culture through a supercentrifuge. The cellular crop was washed 3 times in sea water and resuspended in the same medium. Dehydrogenase activities were estimated by the Thunberg method as modified by Umbreit *et al.* (28). Endogenous oxidation customarily reduced methylene blue in from 30 to 60 minutes, and fatty acid dehydrogenation was indicated by a decrease in the time required for decoloration of the dye when a substrate was added.

Noticeable is the predominant ability of non-sulfate-reducing lipoclasts to dehydrogenate formic acid, none of the cultures failing in this respect. The failures in activation of acids between the heptylic and lauric levels may be due to the toxicity of their salts. Theoretically, the toxic effects should continue to increase with carbon chain length, but the insolubility of salts of the higher acids is believed to have reduced their effective concentrations to subinhibitory levels, and thus to have permitted their dehydrogenation.

The range of fatty acids subject to dehydrogenation by sulfate reducers is somewhat similar to that described above. A difference is observed, however, in the affinity of non-sulfate-reducing lipoclasts for formic acid as contrasted with that of the sulfate reducers for stearic acid. There are the same general limitations to the dehydrogenation of intermediate fatty acids and presumably for the same reasons.

Hydrogen Transfer in the Formic Acid–Linoleic Acid System

The ready dehydrogenation of formic acid suggested that this compound might, upon activation, provide a source of hydrogen for the saturation of other organic substances. Accordingly, a test system was prepared employing linoleic acid as a potential hydrogen acceptor. Data given in Table VI illustrate the progress of the reactions.

Reactants were added to 125 ml. Erlenmeyer flasks, each of which received 10 ml. of $M/15$ phosphate buffer, pH 7.2, and 5 ml. of washed cell suspension. Formic acid, $M/100$, and linoleic acid, $M/200$, were added in 10 ml. quantities and as potassium salts. Distilled water was added, when necessary, to maintain identical volumes in all flasks. The mixtures were prepared in duplicate and incubated *in vacuo* for 24 hours at 27°C. They were then acidified with HCl and extracted with petroleum ether, the solvent being subsequently evaporated under reduced pressure at room temperature. To avoid prolonged treatment in air, no attempt was made to extract the preparations to completion. The iodine number was determined by the method of Yasuda (30). Although the extracts represent both linoleic acid and cellular lipides, the bulk of the material was obtained from the linoleic acid added. Thus, the iodine number is largely a reflection of the degree of saturation of this acid.

TABLE VI

Hydrogenation of Linoleic Acid by Anaerobic Bacteria

Culture	Acid	Extract	
		Grams	Iodine number
XXIX:129–2 (non-sulfate reducer)	Formic	0.0019 .0016	5.3 4.8
	Linoleic	0.0127 .0156	76.2 79.3
	Formic + Linoleic	0.0269 .0125	26.4 29.0
XXIX:136–9 (sulfate reducer)	Formic	0.0011 .0021	7.1 6.5
	Linoleic	0.0207 .0200	81.1 77.5
	Formic + Linoleic	0.0230 .0271	23.0 26.2
XXIX:137–1 (non-sulfate reducer)	Formic	0.0030 .0022	7.0 7.4
	Linoleic	0.0304 .0316	80.7 83.1
	Formic + Linoleic	0.0340 .0355	22.0 19.7
XXIX:137–12 (non-sulfate reducer)	Formic	0.0060 .0071	6.4 5.5
	Linoleic	0.0324 .0346	83.1 80.6
	Formic + Linoleic	0.0371 .0380	23.0 21.6

The hydrogenation of linoleic acid in these redox systems is obvious. Of the four cultures employed, two were known to be capable of dehydrogenating linoleic acid in addition to formic acid, and two were not. Possession of a linoleic acid dehydrogenase is, however, apparently quite unrelated to the ability to saturate the acid, since reduction proceeded with remarkable similarity in all cases.

SUMMARY

Data presented give evidence that fatty acids of the types preformed in nature or released by the hydrolysis of esters can undergo further alteration through the agency of anaerobic bacteria. Organisms tested have been of two general groups: obligately anaerobic sulfate-reducing *Desulfovibrio* and species of facultatively anaerobic lipoclasts which did not reduce sulfates.

The transformation of naturally occurring fatty acids in marine sediments was traced to a limited extent and attributed to the presumable activity of anaerobic bacteria. Saturation of fatty acids buried in sedimentary materials was observed to increase with depth, *i.e.*, with geologic age.

Fatty acids were subject to oxidation by anaerobes. No information was obtained concerning the specificity of fatty acid dehydrogenases, but the ability to dehydrogenate the acids was quite generalized among the anaerobes investigated. Among the important factors affecting dehydrogenation are toxicity and solubility of the substrate.

The pronounced reducing effects of bacterially activated formic acid were sufficient to induce considerable hydrogenation of linoleic acid.

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OBSERVATIONS ON BEHAVIOR IN CAPTIVE FULMARS

By HENRY KRITZLER

The writer collected Pacific Fulmars (*Fulmarus glacialis rodgersii*) in the winter of 1946-1947 in connection with an investigation of the physiology of stomach oil production. Four specimens were secured alive. Since very little concerning the behavior of Pacific Fulmars, wild or captive, has been reported, it seemed worth while to record some of the behaviorisms observed in these birds.

METHODS OF CAPTURE

Two methods of luring fulmars to baits have been employed. The first, less successful than the second, involves the preliminary attracting of gulls, with the hope of exciting the interest of passing fulmars. The collector is lowered in a small skiff from a larger vessel about five miles off shore. As soon as he releases the falls, the ship's cook, by previous arrangement, dumps the previous day's refuse into the sea. That this maneuver immediately attracts gulls in considerable numbers goes without saying. The collector then sets out his baits, which consist of pieces of salt pork each fastened to at least three number 12 treble hooks, which, in turn, are secured to a length of light wash line floated with corks. If there are any fulmars in the vicinity, they are likely to be drawn to the scene by the activity of the gulls. If a fulmar does appear, it wastes no time, as a rule, on the garbage, but immediately investigates the baits, which seem to interest only the more daring, or perhaps, less experienced gulls. The chief disadvantages of this method are interference by gulls and the temporary nature of the lure, that is, the ship's garbage either sinks or is soon consumed.

The second method, which is to be preferred since it attracts petrels but does not excite the interest of gulls, is the salt pork grease method attributed by R. C. Murphy to R. H. Beck. If the sea is very calm, it proves quite reliable. The collector either rows out to sea from shore or is lowered from a larger vessel. In addition to the baited line referred to previously, he is equipped with a small gasoline stove and a considerable quantity of salt pork grease which he has prepared on shore. When he reaches a point far enough off shore to be assured of meeting fulmars (about two miles seems to be enough, although the birds are frequently seen on the seaward edge of the kelp beds), he lights the stove and melts some of the grease. When it is hot and crackling, he pours a little on the sea, and rows on. He sets his course so that when he has created a slick of pork grease a half mile long and a hundred yards wide, he may drift at one end of it. Whale blubber oil was tried, but the film formed by this material was too delicate and was broken up by the slightest breeze. He then sets out his baits and occasionally drops a little more hot grease over the side.

If a foraging fulmar, flying low over the surface of the ocean, crosses the slick, it is as good as in one of the sacks waiting in the bottom of the boat. It will promptly double back and forth, coursing up drift along the slick not unlike a hound on a fresh trail, seeking the source of the fat. When it sees the baits, it will alight on the water, swim up and commence tearing at them without any preliminaries whatever. Such a slick will cause Black-vented Shearwaters to deviate from their courses, but birds of this species are interested neither in refuse nor in baits. The fulmars tear at the baits by grabbing them with the hooked tip of the maxilla and pulling back vigorously. This tendency—to tear their food, rather than to wolf it as do the gulls—results in the birds being hooked by the tip of the beak rather than by the tongue or pharynx. They will duck under for baits suspended under water, but the writer has not seen the fulmar dive.

On February 6, 1947, the writer captured three fulmars in a morning's "fishing." The first bird sighted the slick and came to the baits at 9:00 a.m. It started tearing at them immediately and was so adept at bait stealing that forty-five minutes elapsed before it was caught. Four times during this period the bird was enticed so close to the boat that attempts to snare it with a casting net were made, but each time it darted out from under the mesh. This threat to its freedom was not recognized as such and it was not in any way deterred from returning to the baits. About twenty minutes after its arrival, a second fulmar appeared. Each time the second bird approached the baits, the first fulmar drove it away, actively snapping at the wings and neck of the former. The victim emitted a throaty clucking noise, but the aggressor was silent. At about 9:45 a.m., the first fulmar was caught and placed in a sack, whereupon the second fell upon the baits as though famished and was caught about three minutes later.

Later in the morning, a third fulmar was seen resting quietly on the sea about fifty yards away. A quantity of grease was poured on the water, and as soon as the edge of the slick reached the bird, it swam up and commenced sampling the baits. A minute or two later it was in a sack in the boat.

Of the many extraordinary characters which distinguish the petrels, their utter fearlessness is by no means the least. It is unquestionably a corollary of the adaptation to pelagic life. Mammalian predators probably affect them only during the breeding season and such enemies must be few, judging from the general inaccessibility of their nesting sites. The otic infection which kills hundreds of adults and offshore gales are probably the factors chiefly responsible for holding fulmar populations in check. Bent (1922) cites several references to the trust shown by both the Atlantic and Pacific races. So the fulmar brain probably contains no innate mechanism whereby its owner is apt to respond distrustfully with regard to human beings. The birds are apparently so constituted that, when suitable food is available, they are incapable of associating the manner in which it is presented—in this instance, on hooks—with possible hazard to themselves. Not so, of course, with the gulls. Usually, as soon as a gull perceives that bait is attached to a line, he drops it and moves away. If hooked, the gull seems immediately to associate its predicament with the human on the other end of the line. The fulmars pull back when drawn toward the boat, but with none of the obvious terror which motivates the wild thrashing of the gull. One may hoist a fulmar over the side with no more ado than in landing a smelt, but it takes some exertion to haul in a gull. The petrel seems unconcerned about anything except that somehow it has become entangled. The gull seems to be more aware of the actual state of events. Not until it was grasped by the head did any of the petrels seem to be concerned by the presence of the writer. None regurgitated oil at the time of capture. In the sacks, they constantly poked about, seemingly looking for a way out and occasionally they uttered a plaintive chirp, which, in reality, may have been a sneeze and not a true vocalization. Their activity in the darkness within the sacks is perhaps correlated with the fact that most petrels are normally as active in the dark as in daylight. Gulls are completely quiet, once confined in sacks.

MANNER OF CONFINEMENT

The four fulmars were kept in an outdoor, concrete tank, four feet by eight, with constantly changing sea water at a depth of five to ten inches. As a rule, the birds were separated by wooden partitions, a measure made necessary by the mutual antagonism displayed at feeding time. The tank was enclosed by a double cage of chicken wire which, because the petrels were unable to surmount the walls of the tank, served mainly to protect them from molestation. Each bird was provided with a wooden feeding tray and a wooden platform upon which to rest. Three of the birds showed no concern, at any time, about being confined. Not even when they were evidently hungry did they behave as though they had ever experienced any other environment. The fourth, which incidentally was the poorest feeder and the first to succumb, spent most of its waking hours butting against the wall as though seeking a way out. When the partitions were removed, this bird attacked all of the others with savagery not entirely associated with greed for food. The only times at which the remaining birds showed fear were first, when the writer entered the tank to clean it; and second, whenever he made an unmistakeable move to grasp one of them. His presence at the entrance of the cage seemed usually to be viewed with quiet, alert interest rather than with fear.

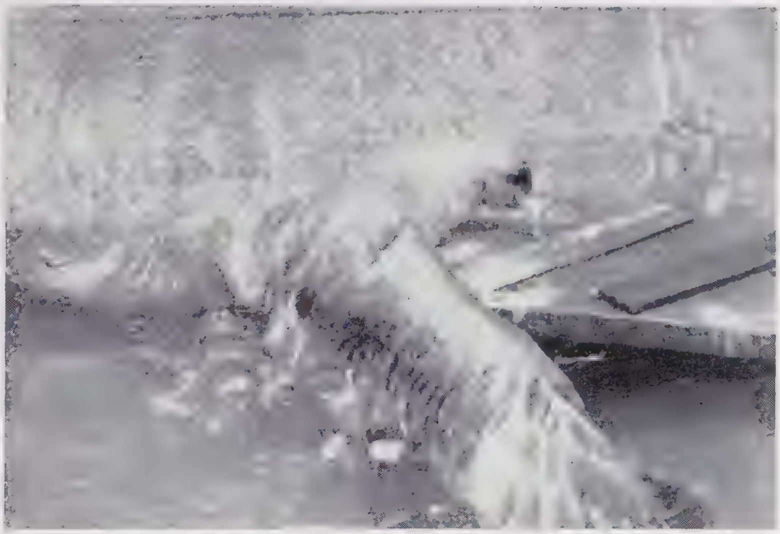

Fig. 1. Captive fulmar climbing on platform.

USE OF THE PERCHING PLATFORMS

The writer was astonished at the alacrity with which the fulmars accepted and made use of the perching platforms. Out of deference to the weakness generally characteristic of procellariiform legs, the platforms were constructed to clear the water by not more than two inches and were equipped with cleats to provide purchase in climbing. At first, the use of the hooked bill and of the wings was indispensable to getting the initial toenail hold in climbing onto the platform. In the future the writer plans to equip the platforms with duck boards extending into the water. The fulmar swims to the edge of the platform, reaches forward and hooks the tip of the maxilla over one of the cleats, paddling vigorously, flaps its wings and finally gets a toenail or two hooked on the edge. Then, still pulling with its beak and using its pectoral appendages as arms rather than as wings, it hoists itself up on the structure (fig. 1). After several weeks of captivity, the fulmar's legs grew strong enough to enable them to hop from the water onto the platform with no help from the bill and only a vigorous flap or two of the wings. When leaving the platform, the birds were obliged to scramble off, but were later able to jump into the water. The fulmars rested on the full length of the tarsi. Occasionally these were raised above the outwardly projecting side feathers as the bird rested on its broad, well-padded ventral surface. This sometimes gave rise to a ludicrous situation arising from the bird's holding itself down by the side feathers when it would attempt hurriedly to rise and get into the water. When the bird elevates itself to stretch or to cackle, it may lift its body on the phalanges alone, the tarsi being raised to an angle of more than forty-five degrees from the horizontal.

When the tank was drained for cleaning, the petrels would stand motionless with the tarsi almost vertical for fairly long periods. When the writer entered to scrub the floor of the tank, a wild panic would usually ensue, the fulmars madly scampering about, tripping and tumbling over one another in their efforts to avoid him. Only the first few steps, in such instances, would be taken on partially extended tarsi.

The eagerness with which the fulmars made use of the platforms is in agreement with the reports, cited by Bent, of the manner in which birds of the Atlantic race scramble onto floating ice when they have eaten so much that they cannot fly. Yet one would suppose that a bird which spends three quarters or more of the year at sea would prefer to rest on the water. It may be safely said that at no time did these petrels actually *rest* on the water in the tank, since they entered that medium only to avoid the observer, to feed, to exercise, or to engage in some other sort of overt behavior. They invariably slept on the platforms, although, in the wild state, they must perforce sleep on the ocean surface at times, at least. Very likely the Pacific birds ride on icebergs also. It would be very interesting to determine whether or not they rest on flotsam in the lower latitudes.

SWIMMING AND BATHING

The fulmar is an agile, if not particularly speedy, swimmer. The remarkable denseness of its ventral plumage which, in good condition, is extraordinarily water repellent and the boat-hull shape of its ventral contours serve to make it extremely buoyant. The upper two segments of the legs are used hardly at all in swimming, motion being restricted to the tarsus and webbed toes almost exclusively. When idling, the legs are fairly relaxed and the tarsi tend to extend laterally as they are waved gently back and forth. When turning and pivoting, they are also extended laterally. But when swimming more energetically, they are extended downward and quite a good deal of thrust is brought to bear in such swimming patterns as plunging in the bath, stretching and exercising the wings, in the peculiar sort of water treading associated with feeding to be described subsequently, and in taking off into flight.

The captive fulmars have demonstrated a remarkable fondness for bathing. One wonders just what sensory impressions evoke the bathing response. One of them was observed to bathe continuously for more than an hour on several occasions. This bird eventually drowned, partially as a result of what seemed to be its inability to satisfy an uncontrollable urge to bathe. The fulmar starts the bath by rearing up repeatedly on rapidly paddling feet, before ducking its head under for the first time. The head is raised immediately after the plunge, water being thrown over the back. The plunge is repeated rapidly, the breast being raised well off the water with the bill depressed before the head and neck go under. When the bird begins to become soaked, the wings are spread on the surface to aid in supporting the body and to give additional purchase in rearing for the next plunge. The birds become thoroughly sodden and bedraggled after some minutes of this, so much so that a good deal of the natural buoyancy is lost. Much of the bird's body then sinks, the use of the spread wings becoming quite essential to prevent foundering. They often become so drenched that they are hardly able to crawl back onto the perching platforms. Two which eventually were found dead in the water evidently succumbed because of inability to regain the safety of the perching platform. That neither of them was malnourished was attested to by the fact that autopsy revealed richer subcutaneous and visceral fat deposits than the writer has seen in *any* bird. It is possible that because the birds received a diet containing a plethora of fat, their lipid metabolism was deranged in the direction of storage at the expense of normal utilization, with a resulting inability properly to anoint the plumage with preen gland wax. The preen glands were fat and one of the birds had produced copious quantities of stomach oil which differed markedly from that described in the literature (see below).

This foundering or wallowing seemed not to diminish the bird's interest in continuing to bathe at all. It is possible that something about inadequately oiled plumage evoked sensory impressions undistinguishable to the birds from those which normally induce bathing in the wild. On the other hand, wild birds may bathe quite as vigorously without encountering the hazard of a thoroughly sodden plumage.

The preening which followed the bath was ordinarily performed on the perching platform. It differed in no noticeable respect from that seen in other birds. The birds were quite able to preen while sitting on the water, as may be supposed.

FEEDING

The diet of the captive fulmars was, for reasons dictated by the physiological experiments for which they were obtained, restricted to hog tissues. Hog lung, liver and heart were given *ad libitum*. The material was cut into small pieces and was placed on the wooden feeding trays. Usually the birds rested on the water while feeding, but if the perching platforms were placed near the trays, they would not always bother to enter the water. Choice morsels would be picked up from the dry concrete floor of the tank when it was drained for cleaning purposes. One bird almost invariably jumped from his perching platform into the water only to scramble out onto the feeding tray, consuming the meal while standing on the full length of the tarsi (fig. 2). If, in his haste, he assumed such a position that his toes only supported him on the tray, his precarious balance was partially supported on half-extended wings. These observations indicate that the fulmar, unlike certain other, more or less primitive sea birds, is capable of recognizing food out of the water. The fact that the feeding trays were used from the first day in captivity shows that this was not due to learning and suggests that when circumstances render it useful, the fulmar may at least clamber upon objects large enough to support it while feeding in the wild.

When the fulmar feeds from the water, it swims up to the tray, selects a morsel, backs away, and proceeds to manipulate it before swallowing it. The food may be shaken from side to side in the water, masticated, and, if it is dropped, retrieved by ducking the head under. The gape is then spread, the mouthful swallowed, and the bird returns to the tray for another morsel. After several have been swallowed, the birds invariably resort to the water treading maneuver alluded to earlier. In this, the legs are paddled vigorously and the entire ventral surface of the bird is raised clear of the water. The wings remain folded, as a rule. Quite a swirl of water passes under the bird as it "treads water." This may be repeated several times before the bird resumes feeding. The frequency with which the behaviorism occurs increases as the meal progresses, until the bird can eat no more. At least two explanations for this behavior pattern occur to the writer. It is possible, on the one hand, that it enables the bird to achieve easy and orderly passage of bulky food particles into the proventriculus, which is a large organ extending throughout the length of the body cavity. Since the sternum is short, the greater portion of this part of the alimentary tract is separated from the exterior only by the thin abdominal wall and the ventral plumage. It is thought that the bird senses the entry of food into this structure and is so stimulated to perform this characteristic response. On the other hand, this performance may only be an homologue of the manner in which the fairly closely related whalebirds cause eddy currents to bring plankton toward their open beaks while feeding. It was mentioned that a considerable swirl of water passes under the fulmar as it "treads water." It may be that, in the wild, fulmars also induce floating food particles to move in their direction in this manner, the mechanism being automatically evoked as an integral portion of the feeding response, whether or not the desired result is achieved.

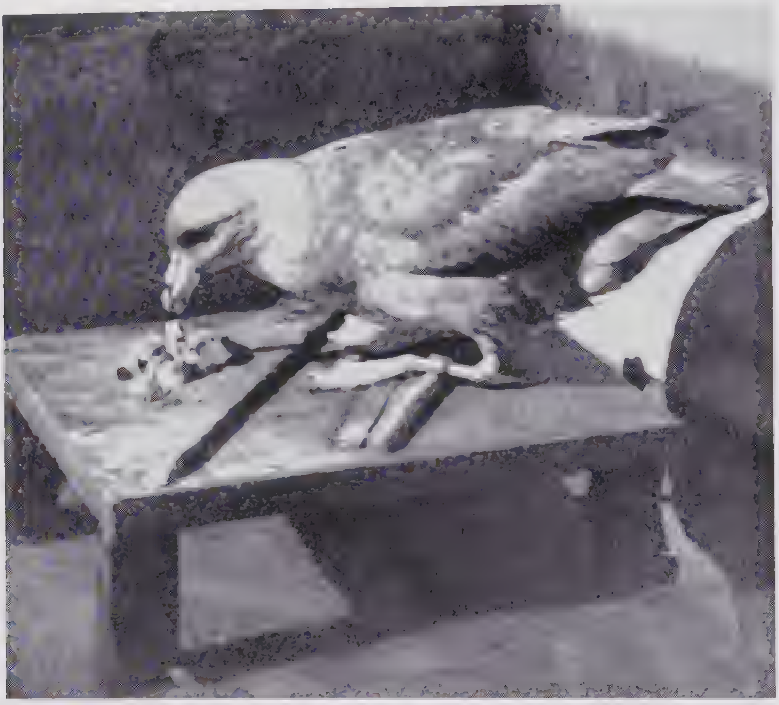

Fig. 2. Captive fulmar feeding on platform.

Sea water is drunk in generous quantities before, during, and after the meal. The water is swallowed directly, without dependence on gravity as seen in most terrestrial birds. When the fulmar can eat no more, it will toy with food for some time before turning its interest to some other activity. A bath frequently follows feeding.

Bent stresses the fulmar's fondness for fatty food. The captive fulmars have rendered excellent substantiation to this report. Out of deference to this character, which seems to be based on a physiological requirement as yet to be worked out, the diet of the captives was always supplemented by small chunks of pure lard. A typical response to this supplement is as follows. As the writer placed chunks of liver, heart and lung on the tray which was, as the bird was well aware, within his reach, the petrel sat on its platform, clucking eagerly and showing great interest in the proceedings, but not daring to come within reach. But when the three or four cubes of lard were dropped on the tray, all fear was forgotten, and the bird literally jumped off the platform, landing with a splash near the tray, to down the lard as fast as this could be done. He would then back away to await the writer's withdrawal before resuming feeding. Those portions of the food which were light colored were selected first. The dark red liver, far more nutritious, and, in fact, more fatty than either the lung or the heart, was left to be eaten last.

From the very first, the petrels were able to select the more desirable lard from among the other morsels, probably primarily because of an innate tendency to choose light colored food, and secondarily because of association processes. Pieces of heart and liver which sank to the bottom at the shallow end of the tank were occasionally retrieved by ducking, but they accumulated in the deep end, where the bottom could be reached only by diving, a maneuver to which they never resorted.

The food was preserved in the freezing compartment of a refrigerator and was therefore very cold when fed. This did not deter the birds from consuming it rapidly, although the body temperature was often sufficiently lowered to cause violent shivering. Although wild petrels often feed with wings extended, the captives usually did so with wings folded.

The writer suspects that, with regular feeding times in captivity, the fulmars became accustomed to responding to food with greater regularity than is probably the case in the wild. Their occasional indifference to food when first caught prompts him to conclude that wild fulmars eat to the point of complete satiation when the opportunity presents itself and will then perhaps ignore food until the enormously distensable proventriculus is once again empty enough to evoke the sensation of hunger.

VOCAL BEHAVIOR

Bent quotes Stejneger as commenting on the "whinnying voice" of the "glupisch," and Captain Collins as reporting that the fulmar (Atlantic race) confines itself to a sort of chuckling sound, somewhat resembling a low grunt. He also quotes Morris who states "The noise that a large flock make is almost deafening, something between the cackle of a hen and the quack of a duck." Bent himself reports observing "a [Rodgers fulmar], presumably a female [that was] sitting on a ledge when a male flew up and alighted beside her; with his beak wide open and his head thrown back until it pointed straight upwards, he slowly waved his head from side to side uttering a soft, guttural, croaking note." This was interpreted as a courtship performance.

The statement is frequently made that the fulmar is a silent bird as a rule, and the writer's observations support this contention wherein it applies to lone individuals. But when others of its kind are about it can be very active vocally. All of the sounds the writer has heard these birds make seem to be derived from a basic croak, perhaps identical with that reported by Collins. This croak may be described as a short, guttural *uck*. When food was presented to the birds the croak was repeated rapidly with the bill almost if not quite closed, the sound becoming a sort of *buck! buck! buck!* When the birds were grasped the croak became a rasping *aaark! aaark!* given through open beak as the bird snapped and struggled in its effort to escape. When one bird was attacked by another, it would emit a *buck! buck!* somewhat similar to that used in anticipation of feeding. But the most elaborate derivative of the croak is what the writer terms "cackling" and which probably is identical with the cackling reported by Morris. When two birds approached one another, the complacent clucking of one would suddenly break into a strident *ăh, ăh, ăh, ăh, ăh, ăh, ăh, ăh, ŭh-ŭh-ŭh-ŭh-ŭh!* As this call was given, the beak was opened fairly wide, the head was raised and the bird's attention was directed toward its companion. The outburst was either greeted by the other bird in kind, or with the more subdued *buck, buck* (fig. 3). Occasionally, particularly on windy days, the petrels were very active vocally and cackling duets were heard repeatedly. The significance of this behavior is as yet unknown. Sometimes, when the cackling had been indulged in for some time, one of the birds, if sufficiently "warmed up" would start "braying." This braying, unlike the ordinary cackling, seems to be produced by alternate inhalation and exhalation, just as in the quadruped with which braying is usually associated. Thus we have an *ăh, ăh, ăh, ăh, ăh, ăh, ăh, ăh, ăh, ŭh-ŭh-ŭh-ŭh-ŭh-ŭh-hongh-ŭh-hongh-ŭh-hongh-ŭh-hongh!* The expiratory honk is deep and resonant.

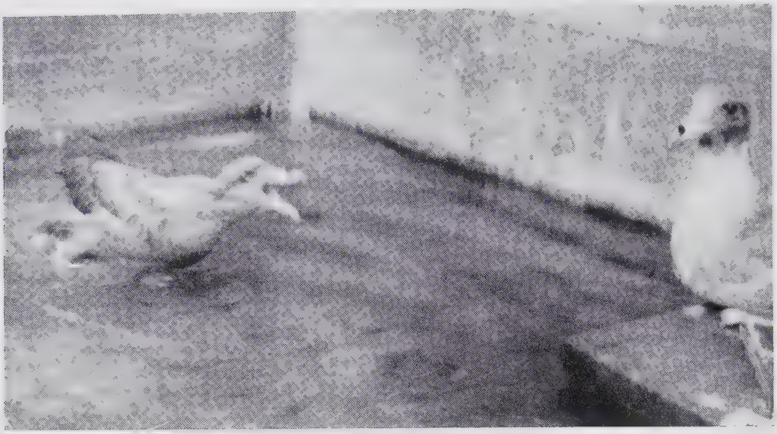

Fig. 3. Attitude characteristic of fulmars while cackling.

Lone birds were never heard to make any sound except the rasping, snarling croak which accompanied their efforts to escape from one's hands. Thus all the other sounds may be ascribed to social responses. The clucking and cackling may be elicited by imitation. The cackling is certainly indicative of an emotional outburst, because while doing so the fulmars may raise themselves, extending the tarsus if perched, or paddling vigorously if sitting on the water, and fanning the air vigorously with the wings. Conclusions as to the significance of these sounds will have to be deferred pending study of the birds in the field.

OBSERVATIONS ON STOMACH OIL

A physiological character which distinguishes the Procellariiformes from other water fowl is the ability to produce in the proventriculus, which is a secretory stomach rather than a crop, a waxy oil which is regurgitated in response to noxious stimuli and when feeding the young. The ornithological literature is rich in references to this phenomenon. Murphy (1936) has presented a concise discussion of the problem, stating that "the function of the oil is not known, beyond the fact that it is discharged as if in defensive reaction, when the birds are approached." He goes on to comment upon the several hypotheses that have been hazarded as to its function. He discounts the supposition that it serves as food for the young on the basis that "the oil does not contain the quantity of protein that would be expected." Yet large quantities of this oil accumulate in the digestive tracts of young petrels, so much in fledgling Atlantic Fulmars that the natives of the Faeroe Islands are said to have used them as candles. When fledgling "mutton birds" are exploited for their oil by the natives of New Zealand, the carcasses are suspended by the head to keep the oil from running out. It must be borne in mind that fledgling petrels and albatrosses, which are usually fed but once daily and which are abandoned by their parents before they are able to fly (three months or more in the Wandering Albatross), have a real problem in water metabolism. When an animal's physiological economy has so evolved that it must depend on the combustion of food for its water supply, an highly adaptive lipid metabolism usually appears. Witness the high fat content of egg yolk, the fat deposits in the camel's hump and in the tails of the Gila monster and the Australian fat-tailed lizard. The enormous fat deposits in female bears which lactate for months during hibernation without feeding are certainly the source of the water secreted in the milk. It is not altogether unlikely that the oil regurgitated by the petrels constitutes the fledgling's water supply. The proteins requisite for differentiation and growth could be supplied in the form of semidigested material regurgitated with the oil. The high hydrocarbon content of the oil would surely provide sufficient energy and water for growth, not to say survival only, when the fledgling has been abandoned on its nest or in its burrow. That there seems to be a relation between the reproductive process and the regurgitation of oil is supported by the fact that the oil has not, to the writer's knowledge, been observed in any of the larger petrels which occur during their respective non-breeding seasons in California waters. No trace of the oil has been found by the writer in healthy fulmars collected in December, January and February, but the captive fulmars commenced oil production in March. It would therefore seem that the possibility that the oil constitutes food for the young should not be ruled out without further study.

Murphy also feels that Hagerup's conclusion that the oil is merely an undifferentiated product derived from the bodies of minute crustaceans is not warranted, since the oil occurs in petrels which have not eaten crustacea and in young birds which have fasted for long periods. It is likely that Hagerup's conclusion was precipitous, but there is a possibility that the oil does arise as a relatively undifferentiated product of partial digestion of not only crustacea but also of other marine organisms, such as squid, which may have fed on crustacea before being consumed by the petrels. The writer has not yet failed to find squid bills either in the proventriculus or in the gizzard of any fulmar or shearwater he has examined. Moncrieff (1946) points out that ambergris, another lipoidal material of musky odor, found in the digestive tract of the sperm whale, an exclusive feeder on cephalopods, is a residue of incomplete digestion of these mollusks. The Merck Index, however, states that ambergris contains about 80 per cent cholesterol, wherein it differs markedly from petrel oil. However, it is possible that there is some relationship between feeding on squid, which seems to characterize most petrels, and the production of the proventricular oil. That there is considerable similarity in chemical composition between petrel oil and spermaceti may be a relevant point (Rosenheim and Webster, 1927).

The proposal of Rosenheim and Webster, who analyzed oil taken from a fledgling Atlantic Fulmar, that it represents an accumulation of preen gland oil (which has a similar composition) hardly seems tenable in view of the absence of stomach oil in non-breeding birds. However, there is no reason to suppose that the stomach oil, when available, does not supplement the product of the preen gland, for indeed, the feathers of freshly collected petrels and, in fact, those of very old petrel skins, invariably smell of the odor attributed to the oil. When petrels are producing stomach oil, it may be present in such abundance that it will bubble and spatter at the nostrils concurrent with respiration (Murphy, Bent).

The fact that petrel oil has a relatively high melting point (it is in fact a wax, rather than an oil) makes dubious the validity of the hypothesis of Green (1887) that the material may be used "to calm the troubled surface of the sea about the birds during severe storms" (quotation from Murphy). For this purpose, an oil which remains fluid at low temperatures is needed.

Rosenheim and Webster showed that the ruby red color of the unsaponifiable matter of fulmar oil is due to carotenes. It was with the view of testing the possible secretory origin of the oil and its pigment that the diet of the captive fulmars was restricted to hog tissues, which contain no carotenoid pigments whatever. Only one brief experiment was performed and that on a single bird. This individual, after it began to regurgitate oil in March, could be relied upon to produce from five to twenty milliliters of oil, when sufficiently provoked, at any time after that. The technique of obtaining the sample is simple. One enters the enclosure with a large beaker in one hand, and after cornering the bird, annoys it with his free hand, by snatching at its tail and allowing it to snap at his fingers. Presently the bird begins to gasp and wheeze. The beaker is placed in front of or over its head, and in a few seconds the sample is violently ejected. If the bird is taken into the hands, there is less likelihood of securing a sample. The regurgitation seems quite involuntary and in no sense may be construed as being directed with reference to the source of annoyance. The occasional appearance of a lump of partially digested food shows that when only oil appears, it does not follow that no solid food is contained in the proventriculus. This ability to regurgitate liquid and retain solids is an extraordinary adaptation.

After several control samples of oil, which on superficial examination resembled nothing so much as rancid pork grease, were secured, the bird was subjected to a course of injections of a 1:9 mixture of alpha- and beta-carotene suspended with the aid of Tween 80 (Atlas Powder Co.) in a minimal volume of 0.9% aqueous sodium chloride. The suspension was injected on alternate days, subcutaneously in the region of the right breast, each dose containing about 2 milligrams of pigment. At the time of each injection and for a period of two weeks after the last (a total equivalent to 12 milligrams having been given), oil samples were secured. No detectable trace of carotenoid pigment was found in any of these samples. On autopsy, prodigious deposits of subcutaneous and visceral fat were found, and the only tissue containing any carotene was the subcutaneous fat overlying the right breast and axilla. The fact that the bird failed to assimilate the injected pigment may have been linked with the almost pathological deposition of depot fat. The unusually fatty diet to which it was subjected may have swung its fat metabolism so far to the storage side that it was incapable of normal utilization. However, the fact that the oil which was regurgitated by this bird more closely resembled pork grease than the petrel oil described by Rosenheim and Webster may lend support to the hypothesis that the proventricular oil is a digestive by-product rather than a secretion.

SUMMARY

Fulmars were caught on hook and line after being lured to baits by the commotion caused by gulls feeding on garbage or by a hot pork grease slick. The petrels took the baits without hesitancy and could hardly be frightened away from them. Consistent with this tameness, while they were still free, was the calm with which they accepted captivity. For birds which spend most of their lives at sea, the fulmars showed a remarkable preference for resting on solid platforms, onto which, at first, they could climb only with great difficulty.

An unusual penchant for bathing was possibly due to abnormal plumage condition resulting from a diet restricted to hog tissues. In feeding, the fulmars showed preference for light-colored food, particularly fat. The birds fed either from the water or while perched on feeding trays. A curious paddling performance associated with feeding was noted.

Four types of vocalization were observed, three of them obviously social in function. No production of stomach oil was observed during the winter months either by wild birds or by the captives, but the oil produced by the latter after the middle of March more closely resembled rancid pork grease than the oil described in the literature. The several hypotheses concerning the origin and function of the stomach oil are discussed.

ACKNOWLEDGMENTS

This study was one of several projects performed by the writer during his tenure as National Research Fellow in Zoology for 1946-1947. To the National Research Fellowship Board in the Natural Sciences, for enabling him to visit the Scripps Institution of Oceanography, and to Dr. H. U. Sverdrup, Dr. D. L. Fox, and Dr. C. L. Hubbs, for the opportunities, equipment and guidance furnished him, he expresses his gratitude. He is also indebted to the Cudahy Packing Company, North San Diego, California, for the donation of the hog tissues fed to the petrels.

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The Scripps Institution of Oceanography, University of California, La Jolla, California, August 20, 1947.

Contribution No. 359

The Aquarium Journal

SWORDTAIL TWINS

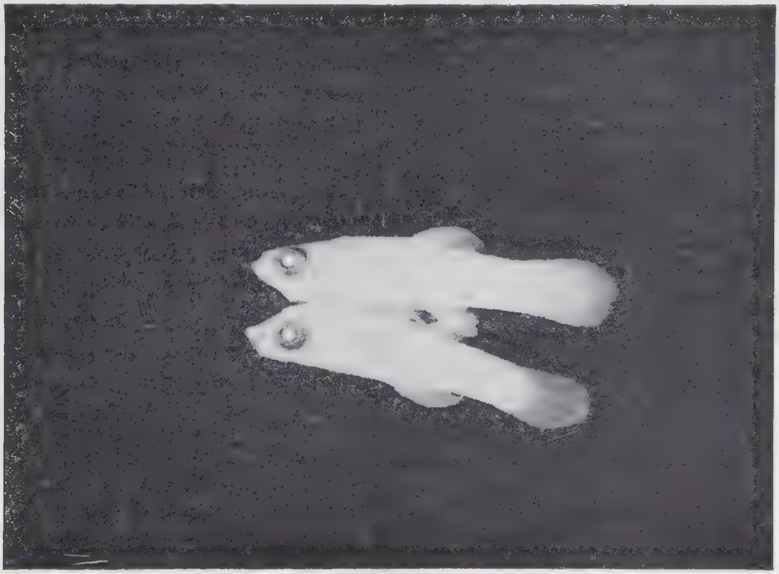
By BOYD W. WALKER

University of California

REPRINTED FROM VOL. XIX, NO. 3

Twins in fishes, particularly of the two-headed type, are not exceptionally rare, but I believe that five pairs of complete twins in one brood sets a record. Moreover, to top it off, one of these pairs lived for seven weeks, which surely makes them runners-up for the old-age record for fish twins.

The brood of red swordtails *(Xiphophorus hellerii)* was called to my attention by Mr. and Mrs. Henry E. Lajoie, proprietors of Lajoies' Tropical Aquarium, Ocean Beach, California. The twins died before I saw them, but the largest pair had been carefully preserved. They were seven weeks old at the time of their death, and about 15 mm. (approximately ⅝ of an inch) long. This length was only a little less than average for the brood from which they came. Both individuals in the pair are complete, and they are joined only in the anterior abdominal region. Twin fishes of this size and age are in themselves unusual, but even more so is the fact that in the same brood of about 60 fish there were four other pairs of twins. Unfortunately, the other twins died at or soon after birth and were not saved, but the Lajoies state that they were identical with the ones which lived.



Paul Williams

Preserved specimens of *Xiphophorus helleri* twins, 7 weeks old, 15 mm long.

The twins were left in the tank with the rest of the brood, and given no special care. One of them is slightly larger than the other, and Mrs. Lajoie says that most of the time this fish swam in a normal position, with the smaller one upside down. At times, however, the fish swam on their sides, and rarely the smaller of the pair was uppermost. During feeding, the larger twin, like the "bully" or dominant fish in a community tank, always controlled the movement until its hunger was satisfied. During this time the smaller fish had to be content with that food which accidentally came its way. When the large one finally stopped feeding, the small one could then take over and control the movements while it fed.

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*Contributions from the Scripps Institution of Oceanography, New Series, No. 359.

The oldest fish twins of this type on record are reported by Rogers[1] from a brood of guppies. He noticed only one pair in his brood, but he was successful in keeping them alive for 14 weeks. Usually such twins die very soon after birth, and it is very rare that they live even for three weeks.

Fish twins such as these arise from a single egg or ovum. Most people immediately refer to them as "Siamese twins." It would be better to compare them with the so-called "identical" type of twins found in humans. Human "identical" twins are joined before birth by a common placenta, but at birth they are separated by the severing of the umbilical cords. The fish twins, unlike their human counterparts, are doomed to be joined throughout life. They receive their nutriment during embryonic development from a common yolk sac, but this is simply absorbed into the body of the fish, and the attachment is not sloughed off as is the umbilical cord. Thus the yolk sac is absorbed by both twins until they are literally "absorbed" together at the region formerly occupied by the yolk sac. Human "Siamese Twins" may be joined in many different regions of the body, and the cause may be different from that of joining in fish twins.

Very little is known about the heredity of monovial, or one-egg twinning. The Lajoies very generously gave me 14 fish from the brood which produced the twins, and these fish are now being bred. It will be of great interest to find out whether the proportion of twins in their offspring is higher than in other strains.

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[1] Rogers, Tom. Guppy twins exceed life expectancy. *The Aquarium,* Vol. V., no. 8, Dec. 1936; pg. 156.

Contribution No. 360

ARSENIC IN THE SEA[1]

By

SAMY GORGY,[2] NORRIS W. RAKESTRAW AND
DENIS L. FOX

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Although the microdetermination of arsenic in biological materials is of interest because of its toxicity, still the determination of arsenic in sea water has received but little attention, despite the fact that most of the marine animals and plants concentrate this element in their tissues. We are in some doubt about the physiological significance of arsenic, as well as about the forms in which it occurs in the sea.

The arsenic content of sea water has been investigated by Gautier (1903), who found about 10 mg./m³., and by Rakestraw and Lutz (1933), who found 9 to 22 mg./m³. Fedossov (1940) investigated the arsenic content of the Azov, Black and Caspian Seas, and found 5.7, 10 and 6 mg./m³., respectively.

Methods. Several methods have been used for the microdetermination of arsenic, but most of these are either not sensitive enough (as the Denigès, Reinch and titration methods), sensitive but not successful for quantitative estimation (as the Bettendorf method), or laborious and cumbersome (as the Marsh method).

In general, these procedures depend upon the separation of arsenic in some form. For example, arsenic is distilled as $AsCl_3$, and then titrated. In the Gutzeit process it is liberated in the form of arsine, AsH_3, which is made to react and produce a stain on $HgBr_2$ paper. Consistent results in the latter case can only be obtained after considerable experience. Nevertheless, this method is still widely used because of its simplicity. Certain modifications in the Gutzeit process have been proposed, such as the replacement of paper strips by paper discs or thread, or the use of constant-area zinc pellets for the generation of hydrogen at a constant rate. The method used in this study is essentially that of Jacobs and Nagler (1942).

Apparatus. The apparatus (Fig. 3) consists of the usual Gutzeit generator, a tube to remove impurities, and an absorption tube filled

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 360.

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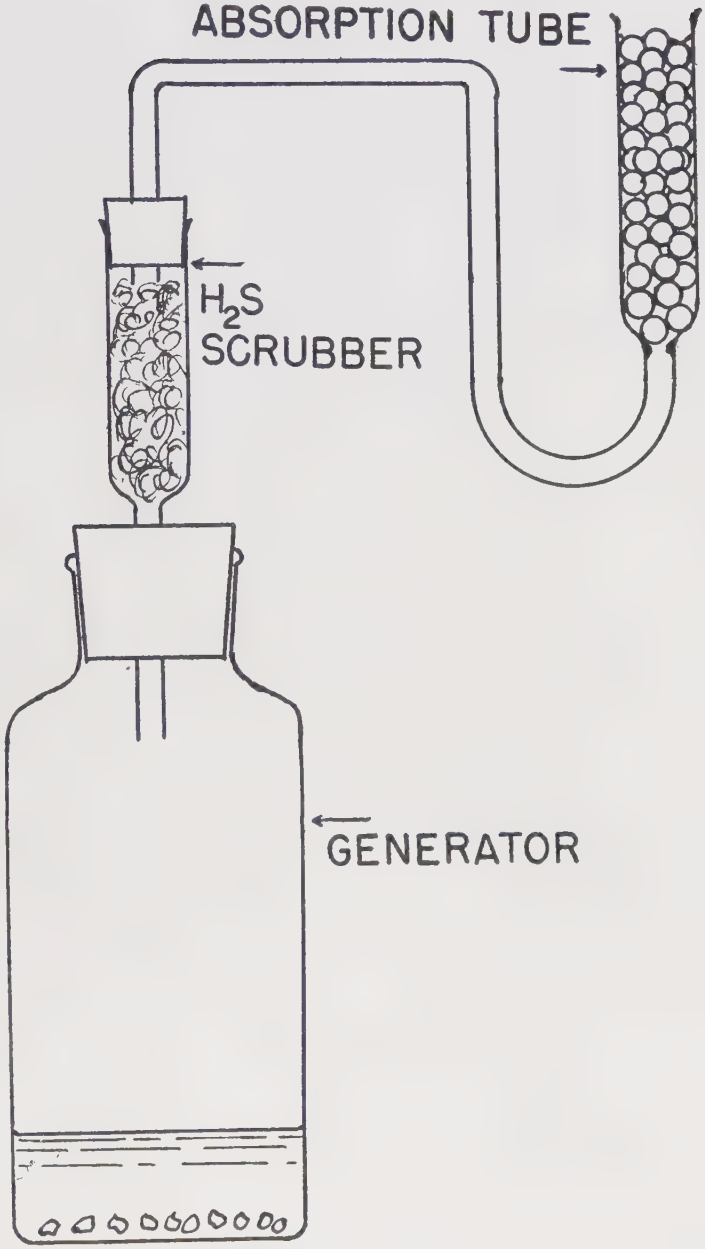
ABSORPTION TUBE
H_2S SCRUBBER
GENERATOR

Figure 3. Apparatus.

assumption that vigorous oxidation destroys all organic matter and that the increased amount of inorganic arsenic found thereafter represents that which was previously combined in organic form and which was not previously revealed by the Gutzeit procedure. It must be kept in mind, however, that this assumption is not certain; for example, there may be resistant inorganic forms of arsenic—ionic or colloidal complexes—which are not thus brought within the scope of the analysis.

A measured sample of the sea water (about 750 ml.) was evaporated on a water bath to about 100 ml. After adding 10 ml. of 30% H_2O_2 and 5 ml. of conc. H_2SO_4, it was further concentrated to half the volume. It was then transferred to a Kjeldahl flask, and the dish washed twice with 2.5-ml. portions of H_2O_2. The flask was cautiously heated until gas evolution stopped, whereupon 2 ml. of conc. HNO_3 was added and the heating continued. At intervals of 10 or 15 minutes, two 5-ml. portions of H_2O_2 were added and the flask finally brought to vigorous boiling until the excess H_2O_2 was entirely decomposed.

The resulting arsenate was reduced with $NaHSO_3$ as previously described and arsenic determined by the modified Gutzeit method and the spectrophotometer.

TABLE II.—VERTICAL DISTRIBUTION OF ARSENIC

Station 9. Longitude: 119° 26.5′ W. Latitude: 33° 0.5′ N.

Depth (*m.*)	*Arsenite*-As (µg. at./L)	*Total* As (µg. at./L)	As^{III}/*Total* As (%)
0	.16	.28	58
10	.20	.32	62
25	.25	.41	60
50	.15	.25	58
75	.11	.19	55
100	.13	.23	56
150	.19	.32	57
200	.16	.29	56
250	.16	.28	55
300	.12	.23	53
400	.20	.37	52
500	.19	.33	56
600	.13	.27	50

TABLE III.—VERTICAL DISTRIBUTION OF ARSENIC

Station 11. Longitude: 118° 48.7′ W. Latitude: 33° 28′ N.

Depth (*m.*)	*Arsenite*-As (μg. at./L)	*Total* As (μg. at./L)	As^{III}/*Total* As (%)
0	.28	.49	57
10	.32	.52	61
25	.25	.43	60
50	.23	.39	59
75	.27	.45	59
100	.25	.43	60
150	.24	.44	56
200	.17	.33	54
250	.19	.36	54
300	.19	.33	56
400	.23	.44	52
500	.19	.35	54
600	.27	.53	50

TABLE IV.—VERTICAL DISTRIBUTION OF ARSENIC

Station 16. Longitude: 118° 42′ W. Latitude: 32° 19′ N.

Depth (*m.*)	*Arsenite*-As (μg. at./L)	*Total* As (μg. at./L)	As^{III}/*Total* As (%)
0	.29	.48	62
10	.33	.59	57
25	.27	.48	60
50	.27	.45	58
75	.25	.43	59
100	.20	.37	55
150	.21	.40	56
200	.21	.41	54
250	.19	.37	52
300	.19	.37	52
400	.25	.48	52
500	.20	.41	50
600	.23	.48	48

TABLE V.—VERTICAL DISTRIBUTION OF ARSENIC

Station 31. Longitude: 118° 06′ W. Latitude: 33° 20′ N.

Depth (*m.*)	*Arsenite*-As (μg. at./L)	*Total* As (μg. at./L)	As^{III}/*Total* As (%)
0	.20	.32	61
10	.25	.44	58
20	.17	.28	60
30	.27	.44	60
40	.24	.41	57
60	.23	.40	57
100	.16	.29	54
150	.19	.32	55
200	.12	.23	53
300	.13	.25	52
400	.19	.36	52
500	.17	.35	50

DISTRIBUTION OF ARSENIC IN SEA WATER

Arsenite-As and total arsenic were determined in water from different depths at four stations, as shown in Tables II, III, IV, and V. Values are given in microgram atoms of As per liter. The results for arsenite-As corroborate, in general, the earlier recorded analyses. There seems to be a slight tendency toward concentration in the upper levels, as well as a definitely higher ratio of arsenite to total arsenic.

Water from one station was used to determine the partition of arsenic among the four forms: arsenite, arsenate, particulate arsenic and dissolved organic arsenic. Results are shown in Table VI.

TABLE VI.—DISTRIBUTION AND PARTITION OF ARSENIC IN A WATER-COLUMN AT Station 28. Longitude: 121° 23.5′ W. Latitude: 33° 5′ N.

Figures are in microgram atoms per liter

	1	2	2−1	3	4	4−2	3+4	5	
Depth (*m.*)	*Inorganic*			*Particulate*	*Filtrate*	*Dissolved Organic*	*Total As*		$\frac{As^{III}}{Total}$ (%)
	As^{III}	*Total*	As^{V}				*Sum*	*Direct*	
0–25	.32	.39	.07	.08	.48	.09	.56	.53	60
50–100	.27	.31	.04	.03	.45	.15	.48	.48	56
150–250	.21	.27	.05	.05	.33	.07	.38	.40	53
300–500	.23	.25	.03	.01	.43	.07	.44	.43	53

In order to obtain sufficient water for the analysis, it was necessary to combine samples from adjacent depths and thus to divide the water column into four levels: 0–25 meters, 50–100 meters, 150–250 meters, 300–500 meters. Five analyses were made on each composite sample, shown in columns 1 to 5 in Table VI.

1. The simple method on the raw water (showing As^{III}).
2. The simple method after reduction (showing $As^{III} + As^{V}$).
3. After oxidation of the suspended matter in a filtered sample (showing particulate arsenic).
4. After oxidation of the filtrate from operation 3 (showing $As^{III} + As^{V}$ + dissolved organic arsenic).
5. After oxidation of the raw water (showing total of all forms of As).

Arsenate-As is obtained by subtracting 1 from 2; dissolved organic As by subtracting 2 from 4. All values are given in microgram atoms per liter.

It will be noted that about 55% of the total arsenic is present as arsenite, about 10% as arsenate, 10% as particulate arsenic, and 25% as dissolved organic arsenic.

It is well known that arsenate interferes with the determination of phosphate, increasing the apparent phosphate concentration proportionally. However, the extent of this interference is apparently negligible in most cases.

ARSENIC CONTENT OF SOME MARINE ANIMALS AND PLANTS

It is well known that marine organisms contain arsenic. The precise part, if any, played by it in their metabolism is uncertain, but it is possible that arsenic enters into the vital activities of the cell.

As a first step, the following marine specimens were analyzed for arsenic: *Octopus bimaculatus* (two-spotted octopus), *Mytilus edulis* (mussel), *Pisoster ochraceus* (ochre sea-star), *Macrocystis pyrifera* (brown kelp).

The samples were dried in an electric oven overnight at 110° C. A known weight was then transferred to a Kjeldahl flask, a 25-ml. mixture of HNO_3 and H_2SO_4 (1 : 1) was carefully added, and the flask slowly heated to foaming. Nitric acid was then added. The rate of addition depended upon the color of the solution, which was not allowed to turn brown. The digestion was continued with the addition of HNO_3 until the solution was water-clear. Heating was continued for an hour longer in order to destroy completely all the organic nitrogen compounds and to complete the removal of all traces of nitric acid. Wet ashing required a long time, especially in the case of the sea mussel and the digestive glands of the starfish; to hasten the process perchloric acid was added when most of the organic material was oxidized. Care was taken to maintain a constant oxidizing condition and to avoid charring, in order to prevent the reduction of pentavalent arsenic, which is generally more easily volatilized.

Arsenate was reduced by heating at about 70° C. with 0.4 g. of $NaHSO_3$ for 60 minutes. The solution was then boiled to expel SO_2. An aliquot was withdrawn, arsine evolved, the color reaction carried out, and arsenic determined with the spectrophotometer. The results are shown in Table VII.

TABLE VII.—Arsenic Content of Marine Organisms

Specimen	*Arsenic (mg./kg.)*
Octopus bimaculatus (tentacles)	0.121 (wet weight)
Mytilus edulis	0.085 (wet weight)
Pisoster ochraceus	1.26 (dry weight)
Macrocystis pyrifera	17.3 (dry weight)

With such a high arsenic content (17.3 mg./kg. dry weight) *Macrocystis pyrifera* is concentrating arsenic as much as 1000 times the concentration of this element in the sea.

Sea anemones, which originally contained 6.6 mg. of As per kg. dry weight, were kept in two aquaria, to which increasing amounts of arsenite and arsenate, respectively, were added from time to time. Individual organisms were removed occasionally for analysis. The concentration of arsenic increased more rapidly in those exposed to arsenite. All animals died after exposure to concentrations up to 90 μg. of As^{III} per liter, at which point they contained 21.2 mg. of As per kg. dry weight. Animals exposed to concentrations of arsenate up to 160 μg. of As^{V} per liter were still alive and contained but 10 mg. of As per kg.

Anemones which had died from exposure to arsenite, as just described, were dried and found to contain 21.1 mg. of As per kg., which was distributed as follows: 91% in the protein fraction (88% being hydrolyzable), 1% in the lipid fraction, and 7% soluble inorganic arsenic. These results must be considered provisional, in view of the small amount of material dealt with.

SUMMARY

1. A modified and improved method for determination of arsenic is described.

2. The total arsenic present in sea water was found in amounts from 0.2 to 0.5 microgram atoms per liter. Of this, from 50 to 60% is in

the form of arsenite, and from 8 to 16% each of arsenate, dissolved organic arsenic, and arsenic in the suspended particulate matter. The relative proportion of arsenite was perhaps slightly greater in the upper levels.

3. The arsenic content of five marine organisms was determined (brown kelp, mussel, sea-star, two-spotted octopus, and sea anemone).

4. The sea anemone was found to tolerate larger concentrations of arsenate than of arsenite. Ninety per cent of the arsenic absorbed from high concentrations was found associated with protein.

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Grant No. 916 (1946), $840. Comparative studies of carotenoid biochromes in marine animals.

The research supported by this grant is part of an extensive general program concerned with the chemistry and metabolism of biochromes in marine animals. Among the organisms under investigation within the project are the octopus, *Octopus bimaculatus,* the highly pigmented, autotomizing sea-star, *Linckia columbiæ,* and the red detritus-eating marine polychæte worm, *Thoracophelia mucronata.* The research is in collaboration with Mr. Sheldon C. Crane and with some assistance from Mr. Bayard H. McConnaughey.

The sea-star, *Linckia,* is, like kindred asteroids, a carnivorous feeder although the nutritive sources of the rich and varied carotenoids in its skin and digestive diverticula have yet to be determined. Meanwhile, chromatographic and spectroscopic analyses have indicated that its skin contains at least five epiphasic carotenoids including alpha- and beta-carotene and some unfamiliar fractions. Six hypophasic carotenoids have been recovered including several which become acidic, as does astaxanthin from Crustacea, upon treatment with alkali in air. The digestive diverticula likewise yields several persistently epiphasic and a number of hypophasic acidogenic carotenoids.

In an attempt to throw light upon the animals' carotenoid metabolism, colonies of this species are being maintained upon diets of (*a*) carotenoid-free food (i.e. hog-liver), (*b*) meat containing carotenes (horse liver), (*c*) flesh of fish containing no carotenes but only xanthophylls, and (*d*) no food.

The octopus, which stores essentially all of its carotenoids in the "liver" or hepatopancreas, loses all such pigment therefrom when maintained for three or four weeks upon carotenoid-free flesh. In this manner it seems to resemble certain animals such as man and the frog in assimilating in its liver any carotenoid fed to it, e.g. alpha- and beta-carotene from horse liver, unchanged xanthophylls from fishes, etc. This condition is reflected in ex-

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tracts of the livers of freshly caught specimens wherein carotenes and xanthophylls are accompanied by unstable acidogenic carotenoids derived presumably from a diet of crustaceans. Investigations are under way in an attempt to verify the source of these latter carotenoids. Xanthophylls and their esters, accompanied by acidogenic carotenoids, but not carotenes, are secreted along with melanin in the ink of *Octopus bimaculatus.*

The red beach worm *Thoracophelia* is in many ways the most interesting animal encountered as regards its carotenoid metabolism. This species contains hemoglobin not enclosed in corpuscles. It ingests much sand along with the marine (mainly plant) detritus of its shore habitat. The beach sand of the worms' environment contains only some 0.7 per cent of organic matter (by ignition). Samples have been found to yield the following quantities of plant pigments calculated in mg. per 100 gm. of organic matter in the sand: chlorophyll 6: phæophytin, 2.3; additional green pigment in the hypophasic extract, 3.6 (i.e. epi- and hypophasic chlorophylloids totaling about 12 mg. per 100 gms.); beta-carotene 0.25; alpha-carotene 0.14; total xanthophylls 8.95 (chiefly fucoxanthin with smaller quantities of other xanthophylls). Thus some 96 per cent of the carotenoids in the worms' food are xanthophylls, but the worms store beta-carotene as the only carotenoid, and apparently not only reject the assimilation of xanthophylls, and even of alpha-carotene, but actually destroy them. The chlorophyll and all but small quantities of its green degradation products are also destroyed by the consumers. Beta-carotene is found in whole worms in quantities of about 0.30 mg. per 100 gms., and in the blood alone in approximately one-third this concentration.

Several yellow neutral non-carotenoid blue-fluorescent chromolipoid fractions are extractable, showing a generally increasing light-absorption in the visible spectrum proceeding from green through blue and into the violet, and commonly exhibiting single maxima in the region from 310 to 300 mμ.

A full account of the carotenoid metabolism of *Thoracophelia* is in preparation for publication elsewhere.

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OBSERVATIONS ON THE MUDSUCKER, GILLICHTHYS MIRABILIS[1]

The mudsucker or long-jawed goby is one of the most important bait fishes used by sportsmen in Southern California. Bait dealers claim this fish is becoming more difficult to obtain and that the demand for it has increased. Several dealers have attempted to culture them for commercial purposes, but have so far met with no success. During the past year I made a study of the development and breeding behavior of the mudsucker (Copeia, 1947, No. 2, pp. 77-85) and investigated the effects of salinity on their spermatozoa (Physiol. Zool., in print). The practical aspects of these studies are summarized here. It is hoped that this may in part aid in the conservation of the mudsucker and perhaps solve some of the problems connected with their artificial propagation.

The spawning period of the mudsucker in the San Diego area (determined from collected young and examination of adult gonads) extends from January to July with the height of spawning in February, March and April. The number of eggs produced by a female ranges from 4,000 to 9,000, depending on the size of the fish. The eggs have adhesive threads at one end. These are attached to a central stalk from which the eggs dangle. The period of development is 10 to 12 days. The young are unlike the adults in that they are differently pigmented and are small-mouthed and large-eyed, whereas the adults have very long jaws and small eyes.

With a little practice it is easy to differentiate a female from a male. The genital papilla of the female is much broader and has a more swollen appearance. Also the papilla of the female is not so pointed at the end.

In numerous attempts I have never been able to strip eggs from seemingly ripe fish. The protracted breeding period and the probability that the females have but one annual spawning make it difficult to obtain a female which happens to be fully ripe at the time. Also it is possible that there must be a ''psychological'' stimulus before the eggs are freely released since the mudsuckers pair several days prior to spawning and exhibit courtship behavior which includes the building of a nest. These factors make the mudsucker an impractical fish for artificial rearing.

Active spermatozoa can be stripped from males during the entire spawning period—January to July. The spermatozoa are active in dilutions and concentrations ranging from 17 percent to 200 percent sea water with a salinity of 33.6 grams per kilogram. They are motile longest in 25 percent sea water. The fact that the bays and estuaries inhabited by *Gillichthys* are subject to an influx of fresh water during the period when this goby spawns may be related to the fact that the spermatozoa are longest active at reduced salinity. However, the spermatozoa are well adapted to the environment of normal sea water as they are active from 3–6 hours in this medium. This must certainly provide time enough for the spermatozoa to find and fertilize the eggs.

As the mudsucker is used so extensively for fresh-water bait, it is well to note that their spermatozoa have no motility in fresh water. This renders them a safe fish to use for bait since, though the fish itself can live in fresh water, it cannot reproduce in this medium. There is no likelihood of its being introduced as an undesirable species in lakes and streams.—*George F. Weisel, University of Montana, Missoula, Montana. November, 1947.*

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NUTRITION AND SEXUALITY IN PROTANDRIC GASTROPODS OF THE GENUS CREPIDULA

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It is well known that the nutrition of the Crepidulas and other fixed or sedentary ciliary-feeding gastropods depends upon the ingestion of minute organisms and particles suspended in the water. These materials are brought to the gill by ciliary action. The water in passing through the gill is filtered through sheets of mucus secreted by the cells of the gill. Many of the suspended particles are caught in this mucus which is then carried by ciliary action through the long food groove on the dorsal surface of the body and thence to the mouth. The larger particles are carried directly to the mouth from the anterior end of the gill, as so fully described by Yonge (1938).

These ingested materials consist of dinoflagellates, diatoms, bacteria and other phytoplankton, together with various kinds of flagellates, ciliates and other protozoa, ova and spermatozoa of invertebrates, and a large proportion of detritus derived from the disintegrated cells of any unicellular or multicellular plant or animal. Particles of sand, of mollusk shells, and other inert substances are included in the stomach contents.

Young individuals have some capacity for locomotion and obtain part of their nutrition by browsing on particles similar to those already mentioned but which may be attached to the substrate. The radula with its many teeth is an efficient organ for this purpose (Coe, 1947).

The question now arises as to the necessity for this nutrition in order that the individual may realize normal sexual development. It should be remembered that all species of *Crepidula* of which the life histories are known normally experience a functional male phase when young and later change to the female phase.

It has been shown by Coe (1936, 1938, 1938a) that the age at which the male phase becomes functional and the duration of that phase varies with the species, with the individual and with the environmental conditions. In this and related genera the functional male phase may be recognized externally by the presence of a relatively large copulatory organ, the phallus, posterior to the right tentacle. This organ usually becomes of functional size only when the gonad has supplied enough spermatozoa to fill the spermatic vesicles. Its outgrowth from the body generally begins with the onset of active spermatogenesis and its retrogression in the phase of sexual transition accompanies the termination of sperm formation. These sexual phases in *Crepidula plana* have been fully and accurately described by Gould (1917).

There are many irregularities and some exceptions to this general rule, for in some individuals of *Crepidula adunca* the phallus has already begun its growth at the time of hatching and before the onset of spermatogenesis. In both *C. fornicata* and *C. plana* the male phase may be aborted experimentally and the phallus is either not formed or it is developed to only a small fraction of its functional size, presumably because of abnormal conditions. This means that the only functional phase, if any, experienced by such an individual is female (Coe, 1936). An older individual, after having passed the period of life when the male phase would normally have appeared, seems to have lost the capacity for inaugurating that phase when conditions for normal activities are restored.

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Not only in mollusks but in all groups of animals and plants, the extent and periodicity of the sexual processes are distinctly responsive to environmental influences. Abnormal temperature, toxic substances in the water, lack of oxygen and lack of food have all been shown to influence both the time and extent of development of both male and female phases in *Crepidula*. The extent, but not necessarily the onset, of the male phase is also influenced by association with another individual in the female phase (Gould, 1917, 1917a, 1919; Coe, 1936, 1938, 1938a).

In *C. plana,* the young snail when it leaves the protection of its mother's foot is only about 1 mm. in length but normally grows to a length of 4 to 6 mm. before beginning active spermatogenesis, with the concurrent outgrowth of the phallus. The increase in size is obviously dependent upon access to the food materials already mentioned. Microscopic examinations show that the sea-water supplied at most marine laboratories, including those at Woods Hole and the Scripps Institution of Oceanography, contains far less of materials required by the young snail than the water before it enters the supply system.

The nutrients available may be sufficient to permit a relatively slow increase in size of the body but without the usually associated development of the reproductive system. The experiment recently reported by Gould (1947) appears to be a good example of such a condition, and similar results have been observed many times in past years. The failure of the young snails to realize sexual maturity in the male phase is presumably not to be construed as due to the lack of opportunity for associating with larger individuals as Gould (1917a, 1919, 1947) supposed but partly to lack of sufficient nutrition. Under similar conditions, but with a suitable food supply, the normal male phase is realized in a large proportion, but not in all, of the experimental animals.

If instead of keeping the young snails in clean dishes of running water they are placed in jars of water containing *Ulva* and the slimy algal growths from other aquaria or mud-covered stones from near low-water level on the seashore, the necessary microorganisms and detritus will become available and normal development often occurs. The snails may be kept separately in vials open at both ends if desired. Mosquito netting tied over the ends of the vial will keep the snail from wandering and the outgrowth of the phallus can be watched without disturbing the occupant. The overflow water from a well-stocked aquarium is also suitable. It is equally satisfactory to keep the open-ended vials or empty mollusk shells in a wire-screened box immersed in the sea. It is common experience that young individuals of oysters, clams, mussels, tunicates and other ciliary-feeding invertebrates cultured in the water at marine aquaria likewise usually realize sexual maturity only when additional food is supplied, although similar individuals develop normally in the open sea.

In nature, *Crepidula plana* occurs not only within large snail shells, often occupied by hermit crabs, but also on other objects, including wooden structures, stones, shells of many kinds and king crabs. In such situations the young may wander far from any other individual. Such solitary individuals are often found in the fully-developed male phase, although their instincts lead them to find another individual if possible. Others are left far behind when a hermit crab carries the mother and her companions away. It is obvious that such isolated individuals although sexually mature, must remain sterile throughout life unless young male-phase individuals find them after they have reached the female phase.

It is concluded from these observations and experiments that the development of the male phase in young individuals of *Crepidula plana* does not require that a mysterious "male-producing stimulus" should be transferred from an older individual provided that an adequate supply of suitable food is available, together with other normal environmental conditions. And this is likewise true of all the other species of the genus which have been investigated experimentally, namely: *C. adunca, fornicata, lingulata, nivea* (*nummaria*), *norrisiarum* and *onyx*. Nevertheless the masculine characteristics are usually more highly developed and are retained longer in individuals that are associated than in those that remain solitary.

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SOME FEATURES OF MELANOID BIOCHROMY IN ANIMALS*

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The most widely distributed of all the biochromes of animals are shades of black, gray, brown, ruddy, tawny, buff, and Tyndall blue. These hues arise from the presence of melanins in various stages of oxidation, in different degrees of physical aggregation and, often, in diverse relations with other chromogenic materials.

Biologists have devoted more attention to the occurrence and distribution in phyla and in tissues, as well as to the genetic and physiological aspects of melanins, than to any other single class of animal pigment. The literature is replete with research papers and reviews given over to various biological questions surrounding melanism. General surveys of chemical and numerous metabolic features of melanin are provided by other contributors to this publication. The present sketch will, therefore, emphasize chiefly: (1) the common biochemical capacity, shared by widely separated members of the animal phyla, for the catabolic derivation of these endogenous dark pigments through enzymic oxidation of tyrosine or related phenolic compounds, and (2) some special morphological and physiological conditions which apply to melanism in certain animals.

Melanins have long been recognized in the fluids of higher plants, such as apples, potato tubers, and the stem-sap of certain species. Similar pigments are also encountered in some species of bacteria and fungi. It was, in fact, from plant tissues that Bertrand (1896) first recovered the oxidative enzyme which he named tyrosinase. This he found to be capable of catalyzing the atmospheric oxidation of tyrosine and other phenolic compounds (*e.g.*, phenol, *p*-cresol, *p*-aminophenol, tyramine, and a series of other *p*-hydroxy compounds) to yield dark-colored polymers (Bertrand, 1907).

Variously colored melanins are present in the ectoderm and endoderm of some coelenterates, such as the dark variants of the plumose anemone, *Metridium senile* (Fox and Pantin, 1941), in the skins of some holothurian and ophiuroid echinoderms, in the integument of certain annelids and flatworms (Verne, 1926; Cloudsley-Thompson, 1946), in the epidermal melanophores and, notably, in the specialized anal gland or ink sac of cephalopod mollusks. Gessard (1902) described the pigment-filled gland within the ink sac of cephalopods. He demonstrated the enzyme tyrosinase in both melanin-free glandular material from fresh animals and the dried sepia sacs sold commercially to artists.

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The integument of some pelecypods (*e.g.*, mussels) and of numerous gastropods is black with melanin. Likewise, the skin and cuticular structures of many insects and a few crustaceans are incorporated with similar pigments.

Among the vertebrates, dermal and epidermal tissues, as well as integumentary derivatives such as hair, feathers, and scales are frequently heavily invested with melanin. The same applies to varicus internal connective or other membranous tissues, *e.g.*, choroid, peritoneum, pia mater, etc., of many fishes, amphibians, reptiles, and birds. Melanotic tumors are of not infrequent occurrence in mammals and cold-blooded vertebrates.

Tyrosinase is present in the tissue fluids of numerous marine invertebrates, including certain sponges (Cotte, 1903), and in even the red and the white variants of the anemone, *Metridium senile* (Fox and Pantin, 1941).

The skin of some newly-hatched insect larvae is very pale, but darkens in a few hours as tyrosinase catalyzes the oxidation and polymerization of the chromogen. This applies, for example, to the cockroach, *Phyllodromia germanica* (Phisalix, 1905), while the pale larvae of the fly, *Musca carnaria,* darken during pupation. Both metamorphosis and melanization may be delayed in the latter, and in other species of insects, by admitting only very limited supplies of air (Dewitz, 1902). Roques (1909) found rhythmic tyrosinase activity in the lymph and fat-body of the developing caddis-fly, *Limnophilus flavicornis.* The enzyme concentration is high at the end of the larval period, becoming rapidly diminished at the onset of the nymphal stage. Later in the same phase, the tyrosine activity is renewed, but is again depressed during the final hours, and seems to be lacking in the adult form.

Gortner (1910) demonstrated tyrosinase in the larva ("mealworm"), pupa, and adult of the beetle, *Tenebrio molitor,* but found the chromogen lacking in the pupal stage. However, the new integument is heavily incorporated with melanin a few hours after the shedding process. Pupae of the locust, *Tibicen septendecem,* on emergence from their seventeen-year residence underground, demonstrate a rapid melanization of the cuticle. This darkening may be delayed by temporary exclusion of air. Water in which metamorphosing pupae of this species had been immersed, was found to have extracted both tyrosinase and the chromogen. Upon exposure to air, the water rapidly became black (Gortner, 1911a). Gortner's (1911b) studies of the Colorado potato beetle, *Leptinotarsa decemlineata,* led him to conclude that the chromogen is probably localized, while the enzyme is secreted over the entire surface of the elytra.

According to Raper and Wormall (1923), tyrosinase plays its role only in the oxidation of tyrosine and other phenolic bodies to a red ortho-quinone, which is converted, through a colorless intermediate phase, to dark, polymerized melanin. Raper and Speakman (1926) demonstrated the identity of this quinone as the primary product of tyrosinase-chromogen systems of the potato, larvae of *Tenebrio molitor,* and the fungus, *Agaricus dryophilus.* The compound is the simplest pigment of the indole class of biochromes, being the 5, 6-quinone of 2, 3-dihydroxy-indole-2-carboxylic acid (Raper, 1927). It occurs in the integument of the marine annelid worm, *Halla parthenopoea costa,* whence its name, hallachrome (Friedheim, 1932, 1933). Friedheim's (1933) characterization of hallachrome as an accessory respiratory catalyst calls for careful reinvestigation.

Figge (1940) has pointed out that the enzymic oxidation of tyrosine to melanin may be regulated by the redox potential of other substances present in or added to the system, and that the reaction may be inhibited by systems whose potential ranges lie on either side of an optimal range between E_0' values of ± 0.3 volts. The presence of a xanthine-xanthine oxidase system inhibits melanogenesis (Fox and Pantin, 1941). According to Lea (1945), the presence of an easily oxidizable compound, ascorbic acid, inhibits the enzymic oxidation of tyrosine. Lea also demonstrated accelerated melanogenesis if the normal physiological levels of NaCl were depressed. He correlated the hypermelanization of the human skin in Addison's disease with decreases in blood-levels of salt, which were, in turn, accompanied by a depression in the ascorbic acid content.

Fresh human epidermis has been shown by Rothman, Krysa, and Smiljanic (1946), to possess water-soluble sulfhydryl substances, lacking in the corium, which inhibit the formation of melanin in tyrosine-tyrosinase systems. The same writers suggest that melanogenic stimuli, such as sunshine, x-rays, and heat or various inflammatory skin diseases may oxidize, or otherwise dispose of, the inhibitory SH compounds, whereupon the enzymic reaction follows readily.

Aqueous extracts of the mushroom, *Lactarius piperatus,* have yielded a crystalline copper-protein (13.6% N and 0.25% Cu) which behaves as a phenol oxidase, catalyzing the formation of melanin from such compounds as *p*-cresol and catechol (Dalton and Nelson, 1938).

Physiological attributes of melanized cuticles of insects have been suggested by Kalmus (1941a & b), as follows: (1) increased protection by the dark pigment against injurious light rays of short wavelength; (2) increased rate of heat exchange, whether by absorption or radiation; (3) enhanced toughness and mechanical resistance; (4) decreased wettability; and (5) protection from desiccation.

The Silky cock, bearing white feathers but black skin, mesenteries, periosteum, pia mater, and intermuscular connective tissues, transmits this pattern of melanism, when bred to a melanin-free hen, only to his daughters (Punnett, 1922). The wattles of Silky fowl are deep purple, resulting from the red color of hemoglobin superimposed on Tyndall blue effects, and accentuated by deeply-lying melanin deposits (see below).

It has been demonstrated by Rawles (1939) that melanogenic skin may be grafted from the postero-lateral head region of embryonic robins to the developing wing of White Leghorn chick embryos, resulting in melanization of the down growing from the transplant in the hatched host. However, the robin's melanophores, having migrated from the grafted tissues into the epidermal collar of the host's feather-germs, express the ruddy color of the donor only until molting. Following the molt, the entire graft bears host-colored (white) plumes.

Axolotls (*Amblystoma mexicanum*) have been shown to generate more melanin, and greater numbers of melanophores, when kept upon black backgrounds, than when maintained in white surroundings (Vilter, 1931a & b). Similar results have been obtained with frogs (*Rana temporaria*) by Dawes (1941), and with fishes, *e.g., Fundulus heteroclitus* (Odiorne, 1933), the guppy *Lebistes reticulatus* (Sumner and Wells, 1933), the long-jawed goby *Gillichthys mirabilis,* and the mosquito-fish *Gambusia patruelis* (Sumner, 1939, 1940; Sumner and Doudoroff, 1937).

Dark backgrounds not only favor the increased production of integumentary melanin but inhibit the deposition of silvery guanine in the skin of the greenfish, *Girella nigricans.* White surroundings, conversely, have the opposite effects. Blinding in both eyes leads to an increase in the integumentary melanin of fishes kept in the light, while mere total darkness brings about a diminution of the pigment in normal fishes and amphibians (Sumner, 1940).

Incontrovertible evidence has been provided, by Sumner (1934, 1935a & b), for the protective value of adaptive coloration of fishes in the direction of concealment. Black and pale *Gambusia patruelis* specimens (having been induced to assume such respective colors by protracted maintenance upon correspondingly colored backgrounds) suffered greater fatalities from attack by predatory birds, *i.e.,* penguins or night-herons, and by carnivorous sunfishes, according to the relative degree to which each physiologically induced color-phase contrasted with black or white experimental tanks.

It has been pointed out that indole pigments of the melanin class are not only responsible for the black and numerous brown shades of color, but they also constitute the basis for some very different hues. Examples are red human hair, ruddy feathers (not to be confused with yellow, orange or scarlet plumes, which usually owe their colors to the presence of carotenoids), the Tyndall blues of scattered light, and the iridescent effects of interference.

Red hair from the human head yields, according to Rothman and Flesch (1943), some 40 mg. per cent of a red, iron-containing, acid-soluble pigment not encountered in other human or non-human hair. The authors have characterized this pigment chemically, and have recorded a single absorption maximum of its acidic aqueous solution at about 535 mμ. They have assigned to it the tentative formula of $(C_{15}H_{20}N_2O_9)_2$ Fe. It would seem highly probable that various proportions must exist between melanins and the red pigment in different shades of red, auburn, or russet-colored human hair.

Nickerson (1946) has conducted comparative chemical and spectroscopic investigations of black and reddish melanins from poultry feathers. He has determined that oxidation of black melanins produces ruddy compounds spectroscopically similar to the natural reddish pigments from red feathers. He isolated, from red feathers, a suspected red melanin, showing a broad absorption maximum in the blue-green region between 530 and 560 mμ and believed by him to be identical with the iron-containing pigment recovered by Rothman and Flesch (1943) from red hair.

Many instances of striking blue skin colors are encountered in animals. Disregarding, for the present discussion, the blue hues of numerous invertebrates, *e.g.*, certain coelenterates, nudibranch mollusks, and crustaceans, wherein conjugated carotenoids are commonly responsible, we shall consider only examples within the vertebrate classes. The pure blues of skin areas in numerous fishes, reptiles, birds, and mammals, including man, and the feathers of many birds, arise from the scattering of incident light which was first described by Tyndall (1869) with reference to the blue of the sky. Sky-blue results from the scattering of short-waved (blue and violet) rays of reflected light by very fine suspended particles, water vapor, and gaseous molecules in very thick layers. Blue light may, however, also be scattered in exactly the same way by very thin layers of media containing optical inhomogeneities whose refractive indices differ markedly from that of the surrounding phase. This scattered blue light is rendered visible if a layer of melanin, or other dark material, underlies the film of colloidal material which is doing the scattering, because the red, orange, and yellow rays penetrate the clear layer and are, therefore, effectively absorbed by the black or brown screen beneath. This leaves the reflected blue component relatively pure in color.

Mason (1923a) pointed out that the mean diameter of the light-scattering bodies must, of necessity, be of the order of the wavelength of visible light, *i.e.*, from 0.4 to 0.6μ. Particles larger than 0.6μ scatter whole white light. While fractionally scattered light is blue, the transmitted light is yellowish or reddish. This may be readily appreciated by comparing blue smoke with its ruddy shadow.

No blue material can be extracted or precipitated from blue pieces of tissue or feather (in contrast to true pigments). Treatment with alkalies destroys the blue color and extracts only dark melanin. Likewise, bleaching the melanin causes the blue color to disappear, but the latter may be restored, in feathers, by applying a substitute dark material, as long as the colloidal scattering medium has remained unharmed.

Tyndall blues have been studied in numerous fishes by Ballowitz (1913, 1914, 1926), and in the blue skin areas of the marine goldfish or garibaldi, *Hypsypops rubicundus,* by the present writer. Bits of blue skin from the tip of the pelvic fin contain transparent iridocytes, filled with their colorless desposits, probably of guanine. No color results where underlying melanin is lacking, but where this pigment is present beneath the iridocytes a brilliant deep blue color is seen by reflected light. Numerous other fishes manifest the same aspect. Among the fishes, amphibians, and reptiles, yellow carotenoids are frequently present in the otherwise clear skin overlying the deeper melanin layers. Under such conditions, the physical blue and the yellow pigmentary colors merge in the manifestation of a complementary green. Removal of the yellow pigment reveals the blue color of scattered light (von Geldern's [1921] investigations of the "Florida chameleon", *Anolis carolinensis,* and the present writer's unpublished observations on some common reptiles).

Certain birds, *e.g.,* turkey, guinea-fowl, and double-wattled cassowary (*Casuarius galateus*), and also mammals, *e.g.,* the muzzle, scrotum, and buttocks of some primates such as the West African mandrill, *Cynocephalus leucophaeus,* and the drill, *Papio sphinx,* and the eyes of man, kittens, and some monkeys manifest the so-called "schemochromic" blues of Tyndall scattering. In these higher vertebrates, the light is scattered by protein systems in the integument, rather than by purines, as in fishes, reptiles, etc. When the epidermis, overlying the deeply melanized corium or other dermal layers, is highly vasculated, purple hues occur, as commonly seen in some of the animals named above. Finally, if the epidermis contains diffuse brown melanin above the coarse black dermal deposits, there result the negroid colors in man and their counterparts in other mammals. Members of the white race have but few melanophores in the dermis and may carry limited quantities of diffuse melanin in the epidermis. The latter may be temporarily increased in quantity by "sun-tanning." Blue "Mongolian spots" in the sacral region of oriental infants are manifestations of Tyndall scattering by clear epidermis overlying dermal deposits of melanin. Familiar to all are the bluish aspects afforded by the presence of venous blood (in veins themselves or in bruises) seen through thin layers of skin. Likewise, the recently shaven jowl of a fair-skinned man may appear blue if the subdermal hairs are sufficiently dark to absorb the longer waves of light. Blue tattoo marks are produced by the injection of inert black pigment beneath the epidermal tissue. In blue eyes, the iris proper is without the melanin which is found in dark eyes. The clear iris, therefore, scatters reflected blue light rays, while the melanized uveal membrane beneath absorbs the longer components. (See Adachi, 1902; Mandoul, 1903; Jordan, 1911; Strong, 1922, 1927; Mason, 1924; Edwards and Duntley, 1939; Cowdry, 1944).

The blue feathers of many bird species have been studied by a number of investigators (Haecker, 1890; Haecker and Meyer, 1902; Mason, 1923a; Gower, 1936; Frank, 1939; Frank and Ruska, 1939) and have been shown to owe their Tyndall effects to the presence, within the barbs, of hollow alveolar or box-cells containing in their walls countless submicroscopic air-vesicles. The absorbing screen of melanin exists chiefly within the walls of medullary cells, lying ventrally and partly laterally adjacent to the alveolar layer. Yellow carotenoids may be extracted from various green feathers, leaving only the Tyndall blue colors. Mason (1923a) outlined diagnostic tests which may readily be applied to blue feathers. Included among such tests are (1) the replacement of air in the minute vesicles of the barb by a fluid of refractive index approximately equal to that of the keratin material of the feather (1.54), such as cresol or phenol; under these conditions, the blue color gradually vanishes, giving way to mere black or brown. Then, upon leaching away the foreign material in a solvent such as alcohol, the blue color is restored at once. (2) The underlying melanin may be removed mechanically or bleached with H_2O_2, thus largely or completely destroying the Tyndall effect. This may be restored, however, by applying a black surface to the ventral part of the barb. (3) Striking a blue feather upon an anvil with a hammer irreversibly destroys the color by squashing the minute air-vesicles and thus disposing of the scattering elements of the system. Tyndall blues may be produced readily in the laboratory by placing dilute colloidal sols or agar gels against black backgrounds.

Finally, reference should be made to the role of melanin in the manifestation of countless "metallic" and iridescent colors found chiefly in the exoskeletons of some insects, feathers of certain birds, the outer skin of reptiles, and the silvery deposits of guanine in the skins of fishes.

It has been clearly established by such investigations as those of the elder Lord Rayleigh (1919), the younger Lord Rayleigh (1923), Süffert (1924), Mason (1923b, 1927a & b), and Anderson and Richards (1942) that these reflected and changeable iridescent colors are due to interference patterns set up in the incident light by its entrance and return through extremely thin laminations, a manifestation of exactly the same principle as applies to Newton's rings, soap-bubbles, oil-films, pearl, old glass, etc. Such iridescent manifestations are greatly intensified if the responsible structure lies over a dark surface (*cf.* a bubble or an oil-slick on a muddy stream or a black pavement), because there results, thus, a minimized dilution of the spectral colors by any light reflected from the underlying substratum. The light impinging upon a dark substratum is absorbed instead, thus leaving the interference phenomena very conspicuous and highly pure.

The integuments and wing-scales of countless insects, including various Lepidoptera, Coleoptera, Diptera, and Hemiptera, owe their brilliant iridescent colors to the presence of multiple thin films of clear keratin, overlying strata of dark melanin. The same principle applies to the relatively flat feather-barbules of such birds as the peacock, humming bird, pigeon, Mallard drake, and many others. Immersion of the iridescent blue wing of the butterfly, *Morpho menelaus,* in media of refractive index close to 1.50, results in an immediate discharge of the bright hue as the fluid replaces the thin layers of air within the scale-structure. Evaporation of the fluid restores the original iridescent appearance at once (*cf.* Mason, 1927b). Feathers and the elytra of beetles, however, contain no interlamellar air and, hence, do not suffer the discharge of their colors. The iridescent appearance may be altered, however, by viewing such structures immersed in highly refractive fluids, or by treating them with swelling agents. The effects induced in such operations are reversible if no permanent distortion of the keratinous structure has occurred (Mason, 1923b). The writer has repeated Mason's experiments involving the removal of melanin deposits from the elytra of beetles by treatment of the lower surface with dilute H_2O_2, resulting in nearly complete discharge of the iridescent colors, and the subsequent restoration of these by painting the ventral surface of the elytra with India ink.

No physiological function of Tyndall blue colors *per se* has been recognized. The melanin alone is capable of protecting underlying tissues from harmful short rays. Furthermore, blue-colored regions of the skin are not only limited in area, but are subject to mutational and sexual differences. It is not impossible that blue feathers might afford some degree of protection against attack by a blue-blind predator, and also that blue feathers and blue skin in birds and mammals may constitute effective sexual adornment.

Iridescent colors present a field of potential attraction for comparative biochemists and geneticists, since the chromatic phenomena observed depend upon the animal's capacity to secrete periodic layers of solidifying materials at particular rates, with definite degrees of thickness (approximating the dimensions of visible light-waves), and involving periodicities governing shape and pattern, to mention nothing of the quantities of melanin associated with the structure and its appearance.

There are, finally, sexual differences to be considered. Pigmentary contrasts between males and females of many species are innumerable and depend upon sex-linked aspects of metabolism. Such classes include the structural blues of some lizards, birds, and primates, since the manifestation of the blue color depends upon deposits of melanin. But sexual dichromatism as applied to the iridescent colors is probably nearly limited to birds, the male being usually, but not always, the more conspicuously colored.

Reproductive activities in birds involve interesting sexual differences in protein metabolism. The female mobilizes much albumin, vitellin, and other proteins to her eggs, while the peacock and male turkey, for example, secrete far greater quantities of protein as "dead" feather-keratins than do their mates. The males, moreover, exhibit striking differences in the manner in which these feather-proteins and the accompanying stores of melanin are deposited in the countless barbules to yield multiple thin films with brilliant optical properties.

More detailed and extensive discussions of the various animal biochromes will later be published elsewhere.

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Conductometric Titration of Chloride in Sea Water and Marine Sediments

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Two applications are presented of conductometric titration equipment described previously. In the titration of sea water, differences between duplicate runs average less than one fifth those of the conventional Knudsen titration, although the time per sample is doubled. In analysis of marine sediment, the accuracy is greater than is actually necessary and the time per sample is one fifth that of the Mohr titration.

CHLORIDE is the most abundant of the ions present in sea water; hence its quantitative determination is useful in many applications connected with the study of the sea.

Perhaps the most fruitful of these applications is in determining the density of sea water. Precise tables (*2*) are available for computing the salinity and the density of sea water from its chlorinity and temperature, when chlorinity is defined as the weight of total halides, expressed as chloride, contained in 1 kg. of sea water.

Although other procedures have been developed, the Knudsen method remains the most widely used by oceanographic laboratories for the routine determination of chlorinity. This modification of the Mohr method uses special volumetric glassware calibrated directly in chlorinity units.

The normal deviation between duplicate titrations by this method is about 0.05%, which causes uncertainties in the density of the same order of magnitude as that caused by a temperature error of 0.05° C. Because oceanographic temperature measurements are good to ±0.01° C., the accuracy of density measurement could be considerably improved if chlorinity data were more accurate. In many instances, such as the calculation of deep sea currents and the preparation of standard comparison sea water, such increased accuracy is important.

The method described in this paper has been found to give duplicate checks to 0.01%. The time required is approximately 8 minutes per complete titration as compared to 4 minutes by the Knudsen method.

Another oceanographic application utilizing chloride analyses is the determination of the water content of marine sediments. The direct procedure of weighing a sample wet and weighing again after oven-drying is often erroneous because of evaporation of water from the sample during storage. A method which has proved more reliable is that of titrating the soluble chloride in a sample and calculating its water content from an assumed chlorinity value. Inasmuch as this value can be estimated within ±1%, the water content values also have this accuracy, which is normally sufficient.

The standard procedure in such titrations is to leach out soluble chloride by repeated washings of the sediment. The Mohr titration can then be used on the clear filtrate.

The procedure described in this paper is convenient because the presence of the sediment in the chloride solution does not interfere with its conductometric titration. This eliminates the need for leaching and reduces the analysis time from 25 to approximately 5 minutes per sample.

EQUIPMENT

The electrical equipment used for measuring relative conductance changes during titrations (*1*) consists essentially of a regulated 1000-cycle source and an off-balance Wheatstone bridge In this type of circuit, the conductance changes register directly on a microammeter. The sensitivity is such that 0.02% change in conductance is easily detectable.

Two conductance cells are used to compensate for temperature rise and any other incidental changes not directly caused by the titration. Each cell consists of a 1-liter wide-mouthed reagent bottle with two pure silver electrode disks sealed to opposite sides of the cell. Construction details are given in (*1*).

PROCEDURE

In titrating sea water, the standard Knudsen 15-ml. automatic pipet and the Knudsen automatic buret calibrated directly in chlorinity units were used. For sediment titrations, a sample (about 10 grams) was dried, weighed, and remoistened with distilled water. It was then transferred into the titration cell and diluted to volume. Coarse sand particles and shell fragments were retained in the weighing dish, as such comparatively coarse particles cause the meter to flicker when they approach the electrode surfaces too closely while being stirred. An ordinary 25-ml. buret was used for these titrations.

Titration. The electrical apparatus including the stirrers is turned on and adjusted as described in (*1*). After a few minutes for the apparatus to stabilize, the conductance of the compensat-

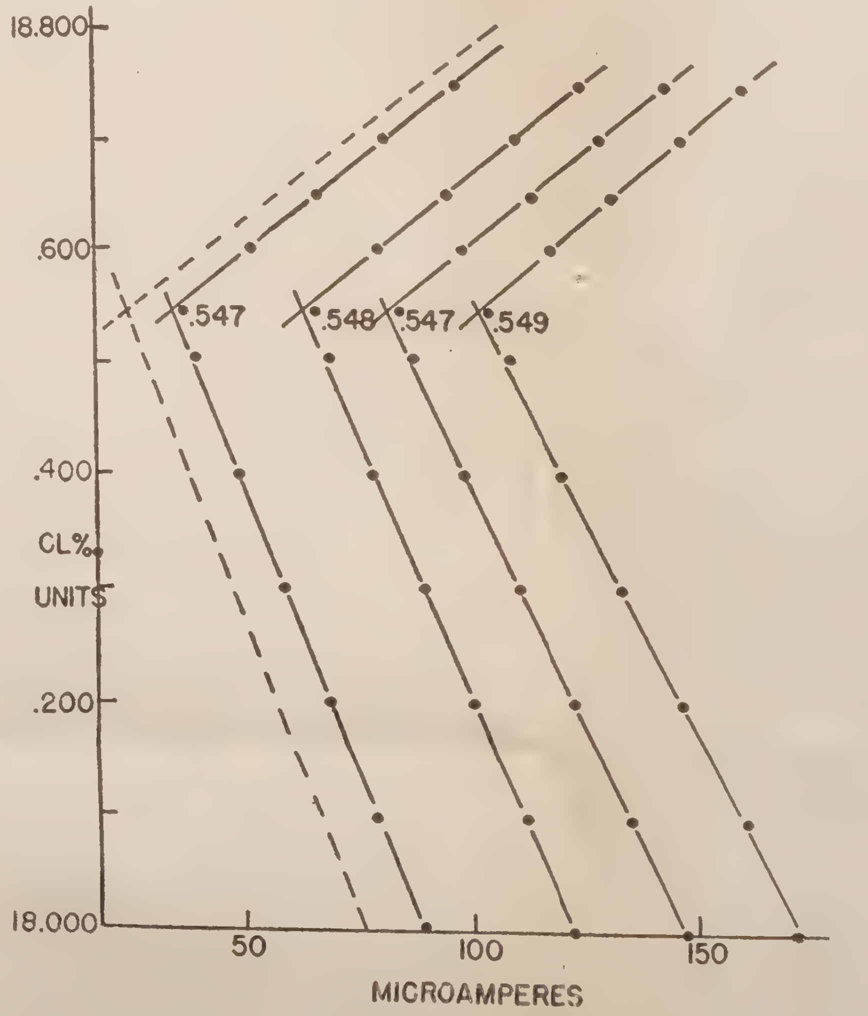

Figure 1

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Table I. Routine Determination of Chlorinity of Sea Water

Bottle No.	Conductometric Method			Knudsen Method			Difference between Duplicates	
	1st	2nd	Av.	1st	2nd	Av.	Cond.	Knudsen
527	18.822	18.827	18.825	18.83	18.81	18.32	0.005	0.020
730	18.908	18.903	18.906	18.905	18.895	18.90	0.005	0.010
550	18.924	18.924	18.924	18.885	18.895	18.89	0.000	0.010
187	18.957	18.958	18.958	18.955	18.945	18.95	0.001	0.010
106	18.998	18.999	18.999	18.97	18.97	18.97	0.001	0.000
526	18.341	18.342	18.342	18.345	18.325	18.335	0.001	0.020
321	18.430	18.433	18.432	18.425	18.41	18.418	0.003	0.015
895	18.445	18.439	18.442	18.43	18.41	18.42	0.006	0.020
401	18.403	18.402	18.403	18.41	18.39	18.40	0.001	0.020
969	18.770	18.771	18.771	18.77	18.765	18.768	0.001	0.005
290	18.739	18.734	18.737	18.72	18.705	18.713	0.005	0.015
463	18.330	18.331	18.331	18.315	18.295	18.305	0.001	0.020
896	18.321	18.324	18.323	18.335	18.31	18.323	0.003	0.025
495	18.333	18.335	18.334	18.33	18.31	18.32	0.002	0.020
197	18.329	18.327	18.328	18.325	18.31	18.318	0.002	0.015
900	18.612	18.614	18.613	18.61	18.60	18.605	0.002	0.010
452	18.773	18.774	18.774	18.755	18.75	18.753	0.001	0.005
296	18.835	18.833	18.834	18.83	18.81	18.82	0.002	0.020
420	18.880	18.876	18.878	18.885	18.87	18.878	0.004	0.015
211	18.917	18.920	18.919	18.905	18.90	18.903	0.003	0.015
						Av.	0.0025	0.014

ing cell is made equal to that of the titration cell by adding to it a sample similar to the unknown and diluting to nearly the same volume. Now the bridge knob is set at its electrical center (previously marked on the dial) and a small amount of water or sodium chloride is added to bring the meter to balance. This adjustment need not be repeated unless samples of widely differing concentration are being titrated. Differences in conductance as high as 25% between the two cells do not cause serious meter drift. The equipment is now ready for the titrations.

The first few drops of reagent are added in order to determine the direction in which the meter will deflect. The balance point of the bridge registers as a maximum meter reading, but the response is not linear within 150 microamperes of balance; hence the needle is set 150 microamperes below balance on the side giving decreasing readings as reagent is added, as shown in Figure 1. In titrations of sea water, or when the approximate end point is known, no readings need be plotted until the end point is approached.

The buret level is now carefully adjusted to a graduation mark within approximately 10% of the end point and this value is plotted against the corresponding meter reading. Subsequent readings are plotted every 0.100 chlorinity unit until the meter readings begin to deflect permanently upscale, indicating that the end point has been passed. Readings are now taken at intervals of 0.050 because of the greater changes encountered after the end point. Three or four points before and after the end point are sufficient to determine its value accurately. As the buret levels were adjusted to graduation marks, buret reading errors are minimized.

Table I is a comparison of a number of duplicate titrations of sea water chlorinity. The average difference between duplicates by the Knudsen method is 5.6 times as great as that of the conductance titrations. Inasmuch as identical glassware and techniques were used in both methods, the greater precision of the conductance titrations is due entirely to the difference in end-point indicators.

Comparison between average values for each bottle shows higher results by the conductance method. The average difference is +0.013. The first Knudsen run agrees better with the conductometric average than the second (+0.008), probably because the technician making the first runs was more experienced than the one making the second runs.

In sediment titrations, where the approximate end-point value is not known, the silver nitrate is added more cautiously. As the end point is approached, the meter needle begins deflecting upscale momentarily with each drop of reagent added. These needle deflections become more pronounced until finally a permanent deflection is observed. After the end point, readings can be plotted for each drop. As with sea water, three or four points before and after the end point are sufficient to establish its value.

In Table II comparative data between the oven-drying method and the conductance titration are shown. In many cases the water contents are higher by the conductance titration method and in a few cases the values are considerably higher, indicating partial drying of the samples during storage.

DISCUSSION

In Figure 1, the abscissa values are proportional to the per cent conductance change occurring in the solution during titration. A conductance change of 1% is equivalent to a meter deflection of approximately 70 microamperes. Before the end point is reached, the conductance of the titration mixture decreases rather slowly. Immediately upon passing the end point the conductance rises with added silver nitrate at a rate three times as great as it previously decreased. If one calculates the conductance changes which should occur on the basis of simple electrolyte theory, including changes in ionic activities, the dotted curve in Figure 1 results. This is seen to follow very closely the observed changes.

Three major effects are present before the end point; silver ion is precipitated as rapidly as it is added, nitrate ion replaces chloride in solution, and the titration mixture is being diluted by the reagent. All of these cause the conductance to decrease. As soon as the end point is passed, silver and nitrate ions are added but none are removed. Because the reagent is considerably more concentrated than the titration mixture, the dilution effect is overcome and the conductance rises rapidly. The tendency of points near the end point to round off may be due either to the finite solubility product of silver chloride or the change in the ionic species adsorbed by the silver chloride. Before the end point, chloride is predominantly adsorbed. As the end point is approached, the chloride concentration becomes low enough to cause removal of the adsorbed ions. Immediately after the end point, silver ions are adsorbed until the precipitate becomes saturated, whereupon the line assumes its true slope. Neither of these mechanisms will cause an erroneous end point if values near the end point are ignored in drawing the intersecting lines.

Table II. Water Content of Marine Sediments

Depth below Surface	Water, Oven Method	Water, Chloride Method
Inches	%	%
0– 3	76	76
3– 6	68	72
6– 9	69	69
9–12	67	67
12–15	60	64
15–18	62	62
18–21	60	60
21–24	58	59
24–27	57	57
27–30	55	56
30–33	55	55
33–36	55	55
36–39	53	54
39–42	54	54

SUMMARY

Conductometric titrations offer an accurate and convenient method for chloride determination. In the titration of sea water, duplicate runs agreed to 0.01%, about five times the precision attained by the standard Knudsen titration, although 8 minutes are required per sample as compared to 4 minutes for the Knudsen method.

The technique is also useful in titrating soluble chloride in marine sediments, as the presence of the sediment in the titration mixture does not interfere. In this case, the titration time is reduced to 5 minutes from the 25 minutes required if the Mohr titration is applied.

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VARIATIONS IN THE EXPRESSION OF SEXUALITY IN THE NORMALLY PROTANDRIC GASTROPOD CREPIDULA PLANA SAY

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TWO FIGURES

A recent abstract by Gould ('47) again raises the question as to whether the young, sexually immature snail of this species must have association with another individual of larger size in order to become sexually mature in the male phase. It was assumed that the question had been satisfactorily answered in the negative by the observations and experiments reported by Coe ('35, '36, '38, '38a) but additional and presumably more conclusive evidence is available and will be presented in this paper. This evidence is based on experiments which differed from those so comprehensively reported by Gould ('17, '17a, '19) and which yielded different results.

It should be recalled that the species of Crepidula and those of the other genera of the Capulidae are typically protandric, most individuals experiencing a functional male phase when young and later changing by a transition stage to the female phase (fig. 1). The latter continues for the remainder of the animal's lifetime. The male phase is characterized by the outgrowth of a long copulatory organ, phallus, behind the right tentacle. This phallus begins its growth with the onset of active spermatogenesis and is absorbed when spermatogenesis ceases before the beginning of the transition stage.

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All these aspects of the normal sexual sequence in C. plana were fully and accurately described by Gould ('17, '17a).

In this species the eggs are deposited in capsules beneath the parent's foot and incubated for about 3 weeks, after which the free-swimming veliger larvae are widely dispersed. Some of them later settle near older individuals and after transformation to the adult form remain in such association. Others attach themselves to a variety of objects and remain solitary unless they later join or are joined by one or more companions.

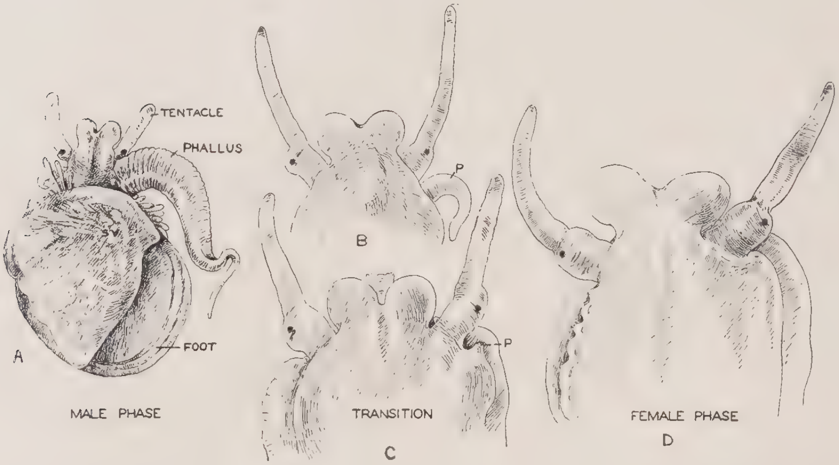

Fig. 1 Consecutive sexuality in Crepidula plana. *A,* functional male phase with unusually large phallus. *B, C,* transition stages, showing resorption of phallus. *D,* functional female phase. (After Coe, '38.)

Examination of the sexual condition of several thousand individuals of this species, representing all ages and at various seasons of the year, supports Gould's conclusion that spermatogenesis in the male phase is more extensive and of longer duration in associated than in solitary individuals. This conclusion has been confirmed for most of the other species studied by Ishiki ('36), Isiki ('39) and by Coe ('36, '38, '38a, '38b) under both natural and experimental conditions.

There is however much variation in the extent of development and duration of the male phase under the same environmental conditions, as Gould has so fully explained. These variations concern the age and size at which active spermatogenesis begins and the outgrowth of the phallus is inaugurated, the duration of both the male and transition phases and the size attained at the beginning of the female phase. Some of these differences are indicated schematically in figure 2 for associated, solitary and experimentally isolated individuals.

Sexuality of associated individuals

Young snails of this species which are associated with larger, female-phase individuals usually begin active spermatogenesis when about 4 to 6 mm in length. The functional male phase may be retained for several months and even for a year or more if opportunities for frequent copulation are present. Most of these individuals begin the transformation to the female phase when 10 to 16 mm long. Gould ('17, '17a) has conclusively demonstrated that experimental isolation of an individual in the male phase usually terminates that phase promptly, after which the transition stage leads to the inauguration of the female phase within a few weeks. In some cases however the male phase remains apparently functional for a month or more after isolation. Unfavorable conditions, such as high temperatures or lack of food, terminate the male phase more promptly.

Among the associated individuals there is a small proportion which appear to retain the male phase throughout a normal lifetime, with no indication that a female phase will follow (fig. 2). These are believed to correspond to the so-called "true males" reported for several species of usually protandric pelecypods and gastropods. It is suspected that they may have a somewhat different genetic composition from those that more frequently remain solitary, as well as associated individuals that have a relatively brief male phase (Coe, '43, '44). About 90% of the young snails became functional as males when associated with female-phase individuals under experimental conditions.

Sexuality of solitary individuals

Upwards of 10 to more than 20% of the population in some situations consists of individuals which have remained solitary, either by chance or by choice, and in most of these the period of active spermatogenesis and the retention of the male phase, if developed, is comparatively brief (fig. 2).

In some situations each of these solitary individuals is the sole occupant of the empty shell of Crepidula fornicata or some other dead gastropod and so widely separated from other members of the population that association has been

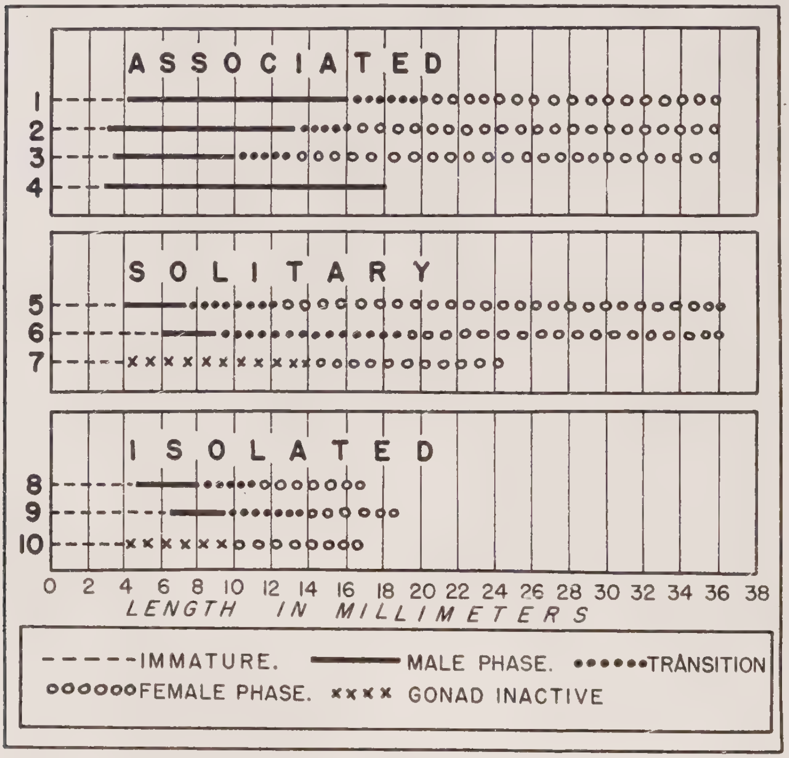

Fig. 2 Schematic representation of the variations in sexuality of Crepidula plana when associated and when solitary, as found in nature, and when isolated experimentally before visible sexual differentiation. Line 4 represents one of the so-called "true males." Lines 7 and 10 indicate individuals in which the male phase is abortive. (Modified from Coe, '36.)

impossible. Nevertheless the masculine characteristics may become fully developed. In some of these solitary individuals the relatively brief male phase is followed by a long transition period, during which growth is usually much more rapid than in either of the functional sexual phases. In others neither spermatogenesis nor phallus outgrowth occurs and microscopic sections indicate that the young gonad remains in an immature and inactive condition for several weeks.

Under favorable conditions the gonad may then resume activity but with the production of ova instead of spermatozoa as is usual in the first functional sexual phase. In such individuals the normal male phase is completely aborted (fig. 2). After reaching the physiological age which is normal for the onset of the female phase, the animal seems to have lost the capacity to inaugurate a normally preceding male phase. It is evident that either of the sexual phases can be inhibited but the sequence cannot be reversed. Individuals which have been solitary in the male phase are usually found later by younger males and thereby become fertile in the female phase. It has been proved for one species of the genus that after the spermatic receptacles have been filled, an isolated individual in the female phase may continue to produce fertile eggs for a year or more (Coe, '42).

Sexuality of isolated individuals

It was concluded by Gould ('17, '17a) that the realization of the functional male phase in this species requires a more or less intimate association of the young animal with a larger individual in either phase of sexuality. It was found that actual contact was not necessary and Gould ('19) concluded that some kind of a male-producing stimulus was transferred through the water from the larger to the younger individual. Some years later Coe ('35, '36, '38) reported that such association, although usual, was not an invariable prerequisite for maleness. He found that some of the solitary and isolated young, if kept under normal conditions of food and temperature, experienced the normal male phase if far removed from any larger individual.

In a recent abstract Gould ('47) reported his failure to obtain normal male development in young individuals kept in dishes of running water in the laboratory. Some of his experimental animals experienced an incomplete development of maleness, indicated externally by a stumpy fundament of the phallus after a period of about 30 days under experimental conditions. No further development occurred and the fundament was absorbed after a short time. Under these conditions some of the individuals only 1 to 5 mm long at the beginning of the experiment reached a length of 14 or 15 mm after 40 days. At the latter size the female phase normally begins.

It seems evident that Gould's failure to obtain the usual male development in some of his experimental animals must have been due to the abnormal conditions under which his experiments were made. Similar experiments conducted by the present writer in the same laboratory at Woods Hole during the summers of 1934 and 1935 and continued later at Yale University resulted in the production of apparently functional male-phase individuals in a large proportion of the experimental animals of the same sizes and same species. These experiments differed from those of Gould however in that the young snails were provided with an abundant food supply.

The Crepidulas, as is well known, obtain their nutrition by the ingestion of minute organisms and particles suspended in the water. These materials are caught in sheets of mucus as the water passes through the gill and are then carried to the mouth by ciliary action. The ingested substances consist of algae, diatoms, dinoflagellates and other phytoplankton, together with various kinds of flagellates, ciliates and other protozoa, ova and spermatozoa of invertebrates, and a large proportion of detritus derived from the disintegration of the cells of any unicellular or multicellular plant or animal. Young, motile individuals obtain part of their nutrition by browsing on materials similar to those mentioned.

Although the snails may live for several months on the small amount of nutrition available in the laboratory's water supply and increase considerably in size, additional food seems to be necessary for normal sexual development. This can be furnished by the growths of small algae and associated organisms which grow on the walls of large aquaria or by the organisms and detritus in the slimy mud at the low-water level along the seashore.

Since the problem involved the question as to whether normal male development occurs without the association of the sexually undeveloped young snail with another individual of the same species, the experimental indivdiuals were cultured in separate wide-mouth vials. To insure the free circulation of the water the vials were open at both ends but covered with mosquito netting to prevent the occupant from escaping. The vials were then suspended in a large tank supplied with food as mentioned. Running water, aeration and Ulva were provided. The young snail soon attaches itself to the side of the vial and the development of the phallus can be observed without disturbing the occupant.

To insure against the possibility of a previous association, only those young were used which were solitary when collected. Under such conditions 14, or nearly 30%, of the 48 young snails, which were 3 to 6 mm in length at the beginning of the experiment, with no indication of phallus, developed into apparently functional male-phase individuals within 6 weeks. Microscopic sections of several of these showed normal spermatogenesis and filled spermatic vesicles.

Even with these provisions for food and aeration, the conditions in the laboratory were evidently not as favorable for sexual development as the natural environment in the sea. This was proved by placing 63 young of sizes similar to those mentioned, and of the same origin, in separate vials, prepared as in the preceding experiment, and placed in a wire-screened box. The box was suspended in one of the large ''live cars'' in the harbor and with free circulation of the water. No less than 29 of these, or 46%, developed an apparently normal male phase. In several of these the male phase was retained for more than 20 days. Fourteen of the others formed only the fundament of the phallus and showed arrested spermatogenesis. In the remaining 20 the gonad remained inactive for several weeks and showed female development thereafter. Those with the inactive gonads increased in size more rapidly than the others.

Under the conditions of this experiment nearly one-half of the experimental snails developed the male phase without associating with any other individual but the remaining 54% are equally interesting. Since it is well known that association with individuals in the female phase accentuates and prolongs the male phase, as Gould ('17, '17a, '19) and others have so definitely proved, it seems probable that the 14 individuals with arrested male development would have become functional if opportunity for mating had been provided.

It should be emphasized however that nearly one-third of the young snails showed no visible evidence of the male phase, although they had been cultured under as natural conditions as could be devised except that association with other individuals had been prevented. The question still remains as to whether they would have omitted the male phase if they had remained solitary in their natural environment. Coe ('38, '38a) presented evidence that in this and other species either of the two sexual phases could be inhibited by unfavorable chemical or physical conditions.

The experiments here recorded differed from those reported by Gould ('17, '17a, '19) in that all of the young were solitary when found and none of them came from shells occupied by hermit crabs. They also came from a different locality. Perhaps these facts should be taken into account in considering the discrepancies in the results.

There seems to be no satisfactory evidence that the accentuation and prolongation of the male phase by association is due to any masculinizing chemical substance which might pass through the water from the body of the individual in the female phase. It seems more probable that the influence is a reflection of the stimuli received by the male through his sense organs, presumably those of tentacles and phallus. It is conceivable that these stimuli and their nervous responses may influence the masculine characteristics of the male-phase individual, perhaps by the mediation of substances secreted within his own body. Possibly the same conditions may apply to some of the sexually undifferentiated young.

It will be observed that a larger proportion of the experimental animals which were kept in the outside water developed the male phase than did those which were cultured in the laboratory. But it is improbable that even the former were as favorably situated for sexual differentiation as the solitary individuals in nature. It is conceivable that an experiment might be devised which would more closely approach the natural conditions and in which more than 50% of the isolated young could be expected to develop the male phase. But that all of them would, seems doubtful. That nearly all individuals have the capacity to do so if appropriately associated seems to be in harmony with the experimental evidence.

In this and other species, some of the associated young individuals reach the male phase at a smaller size than is usual in those that remain solitary. It seems quite possible that this is due to the early development of masculine instincts in some individuals which lead them to seek such association when smaller than their contemporaries. It is well known that active spermatogenesis is accompanied by a decreased growth rate.

Sexuality of other species

In all but one of the 8 species of Crepidula studied by Coe ('38, '38a) intimate association or permanent mating with one or more individuals in the female phase tends to accentuate the masculine characteristics and to postpone sexual transformation by prolonging the male phase. In 7 of these, namely: C. adunca, C. convexa, C. fornicata, C. nivea (nummaria), C. norrisiarum, C. onyx, and C. plana, the influence of association is conspicuous; in C. lingulata it is less obvious. It is also conspicuous in C. aculeata and C. walshi of Japan, as reported by Ishiki (Isiki, '36, '39), as well as in Crucibulum spinosum (Coe, '38b) and in C. imbricatum.

In all species with these characteristics, as Gould ('17) has shown for Crepidula plana, the ratio of male-phase to female-phase individuals is much larger when the animals are associated in colonies than it is when the individuals are solitary, for the reason that the time spent in the male phase is longer in the former case than in the latter, in addition to any tendency of the male phase to become abortive when solitary.

In all these species and in some other normally protandric mollusks, both gastropods and pelecypods, there seems to be good evidence that some individuals have a stronger tendency toward one sexual phase than the other. It has been suggested that differences in the genetic composition may account for the variations in sexual differentiation and behavior in different individuals of the same species (Coe, '43, '44). Experiments with several species of Crepidula indicate that some young individuals remain solitary in the presence of abundant opportunities for association. In these the male phase, if developed, is comparatively brief and they are thought to have inherited a strong female tendency. A few others are so strongly masculine that they retain the male phase even after several weeks of isolation.

There are other examples of usually protandric mollusks in which a small proportion of the population is strictly unisexual, the so-called "true males" and "true females." Among them may be mentioned the snail Patella coerulea. Bacci ('47) reports in a recent paper that about 92% of the several thousand individuals examined were protandric, the other 8% being strictly males or females. Whether this inhibition of one of the alternative sexual phases results from genetic or from environmental influences is not at present known. In some species of mollusks there are local races with differing hereditary types of sexuality. One race may be bisexual and another unisexual.

In some gastropods with consecutive sexuality a primary male phase is succeeded by a functionally bisexual condition and this is followed by a final female phase. The pteropod Limacina as described by Hsiao ('39) is a good example of such a transition from male to female phase, with a gradual accentuation of the feminine characteristics.

Influence of nutrition

In comparing the results of Gould's ('19, '47) experiments with those reported in this paper it is evident that an abundant food supply is necessary for normal sexual development. This is in harmony with the general experience in culturing animals and plants under aquarium conditions. Microscopic examinations of the sea water supplied at the Woods Hole laboratory, as well as at other institutions, show that it contains much less material suitable for the nutrition of Crepidula than the water before it enters the supply system. The amount may suffice to allow the continued growth of the animal, although it may be insufficient for normal sexual maturity. Other ciliary-feeding invertebrates, including clams, mussels, oysters, and tunicates, when cultured in the aquarium without an additional food supply usually remain sexually immature. Furthermore there is some evidence that the amount of food available may influence the type of sexuality in mollusks, both gastropods and pelecypods. In the normally bisexual slug Agriolimax it was found by Richter ('35) that abundance of food was conducive to the production of ova, while only spermatozoa were formed and the gonad appeared to be exclusively male after long starvation.

In certain unisexual mollusks the females not only live longer than males but they are larger at the same age. Localities and seasons favorable for rapid growth sometimes have a large preponderance of females (Coe, '43). In both invertebrates and vertebrates, as well as in some plants, the quality as well as the quantity of the food profoundly affects the sexual conditions.

Genetic basis of consecutive sexuality

The genetic basis for all these examples of protandric consecutive sexuality obviously depends upon the determination of all individuals for both the alternative phases, with associated factors which determine that the male phase shall normally become differentiated first. This is accomplished through the earlier activation of the spermatogenic constituents of the primary bisexual gonad. Correlated with the development of the spermatic tissues occurs the outgrowth of the phallus and the differentiation of the spermatic vesicles. Associated also are such instinctive patterns of behavior as are characteristic of the functional male phase.

The second, or transitional, sexual phase is inaugurated by the cytolysis of the spermatogenic tissues, associated with or followed by the growth of some of the ovocytes formed in the primary phase and the degeneration of others, as well as by the proliferation of ovogonia. The absorption of the phallus, the differentiation of the seminal receptacles, oviduct and yolk deposition follow, with correlated behavioristic instincts.

The third, female, sexual phase is the climax of the sexual cycle, with functional activity of the newly formed morphological and physiological differentiations. In this phase the individual which was so actively masculine in youth, now accepts her mates, deposits her eggs and incubates her young beneath her body. Each of these events is evidently a response to a preceding action and in turn initiates the one that is to follow.

Experimental evidence, as well as observations in nature, indicate that any of these phases may be abbreviated or prolonged by environmental conditions but that the sequence cannot be reversed except to a very limited degree.

It was mentioned that in all the species studied, isolation of the associated male-phase individual usually, but not invariably, terminates that phase and inaugurates the female phase within 1 to 3 weeks. This experimental change of sex is merely the precocious realization of the sexual phase which would otherwise have been experienced somewhat later in life. It is comparable with forced metamorphosis from the larval to the adult condition in insects and some other animals.

SUMMARY

1. In Crepidula plana, as in other species of the genus, the majority of the population consists of individuals which are more or less closely associated in small groups. Each group commonly contains 1 or more individuals in the female sexual phase, accompanied by several younger animals in the immature or functional male phase.

2. In some situations 10 to 20% of the population consists of individuals which have remained solitary, either by chance or by choice, and some of these likewise experience a brief normal male phase.

3. When sexually immature solitary young were cultured separately in the aquarium with a plentiful supply of food and with other conditions as nearly normal as possible, except for lack of association, nearly 30% of the experimental animals developed an apparently normal male phase.

4. After similar isolation in bottomless shell vials immersed in the sea, 46% of 63 young developed an apparently normal male phase within 6 weeks; in 22% the male phase was arrested and aborted without completion. In several of the former that phase was retained in apparently functional condition for about 3 weeks. In 32% the gonad remained inactive for several weeks and later developed the female phase.

5. The normal male phase was developed in about 90% of the young which were associated with individuals in the female phase.

6. It is evident that association of the young with a larger individual, although usual, is not a prerequisite for the development of the functional male phase. It seems quite probable however that some of the young snails which remain solitary and in which the male phase is aborted would have become functional in that phase if opportunity for association with a large individual had been afforded.

7. Isolation of associated male-phase individuals usually terminates that phase and inaugurates the female phase within 1 to 3 weeks in this and 6 other species.

8. The variations in the expression of sexuality under the same environmental conditions suggests that there may be individual differences in genetic constitution.

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Contribution No. 369

THE GREAT BASIN

With Emphasis on Glacial and Postglacial Times

II.

THE ZOOLOGICAL EVIDENCE

Correlation between Fish Distribution and Hydrographic History in the Desert Basins of Western United States

BY

CARL L. HUBBS and ROBERT R. MILLER

THE GREAT BASIN, WITH EMPHASIS ON GLACIAL AND POSTGLACIAL TIMES

II.

The Zoological Evidence: Correlation between Fish Distribution and Hydrographic History in the Desert Basins of Western United States[1]

Carl L. Hubbs and Robert R. Miller[2]

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 369. This paper is an elaboration of our contribution to the symposium that was read on June 16, 1942, in Salt Lake City, Utah, at a meeting of the Pacific Division of the American Association for the Advancement of Science in which the Western Division of the American Society of Ichthyologists and Herpetologists participated. We incorporate conclusions from field and laboratory studies made after the paper was read and we refer to the recent literature.

[2] When this paper was read the authors were on the staff of the Museum of Zoology, University of Michigan. They are now connected, respectively, with the Scripps Institution of Oceanography and the United States National Museum.

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INTRODUCTION

We are now convening deep below the surface level of an ancient inland sea. The shore features of Lake Bonneville still scar the mountain sides about us. The evidence for the existence of this great water is as convincingly clear as are the indications of Pleistocene glaciation, and the two phenomena are now thought by most geologists to have been at least approximately coincident. This correlation has just been laid before you, along with a masterful synopsis of the geological history of the Great Basin.

Evidence of Pluvial Conditions

It remains to be shown how convincingly the physiographic deductions are supported by our knowledge of the distribution of life in the Great Basin. In correlating the geological and biological evidence, particular attention will be paid to the fishes for two reasons: first, since fresh-water fishes are intimately confined to the waters that they inhabit, they reflect precisely the changing hydrographic history; second, the fishes have been the special object of our own researches in the region (Hubbs, 1941*a*; Miller, 1946*a*).

Whether viewed through the eyes of physiographers and glacial geologists or through those of biologists, the Great Basin is a land of relicts. Throughout the vast and generally arid expanses between the crests of the Wasatch and Sierra Nevada ranges physiographers observe remnants of moist land and of water, and in these habitats biologists find isolated populations of plants and of animals (for example fishes—Hubbs, 1941*a*). Physiographers tell us that in the geologically near past the Great Basin was a well-watered land, and biologists have accumulated a large body of evidence which indicates that the relict biotas were interconnected. At a relatively recent time, geologically speaking, the now parched desert bolsons that separate the habitats of the moisture-loving or water-confined animals and plants were no doubt sufficiently moist and cool to allow the passage, if not the continuous range, of types of organisms that are not adapted to desert life. That the deserts were more copiously watered in very recent geological time must be evident to any keen observer as he travels through the region. Shore features of ancient lakes extend in horizontal lines around many of the enclosed basins, far above the level of the ephemeral lakes and of the playas. Scars of long river courses, now dry except in rare and local floods, cut through and between the desert hills. Numerous travertine deposits give mute evidence of hot springs that once gushed from the now arid hillsides.

Geologists agree that the last Pluvial period provided conditions that were suitable for the wide dispersal of faunas and floras. We are almost forced to assume, for example, that this was the time when certain oaks and their associated gall wasps, characteristic of the California region, must have crossed the now oakless intervening deserts to reach their present locations on the mountains to the eastward (A. C. Kinsey, personal communication). Each of the numerous local forms of the moisture-requiring pocket gophers that inhabit springs and mountain meadows in the desert regions "may appropriately be looked upon as a relict form from earlier times when conditions of moisture were much more generally prevalent in the Great Basin territory, and when the dependent fauna and flora were correspondingly widespread" (Grinnell, 1926). It was surely then that fish populations were able to reach the many remote springs and creeks that they now inhabit.

It is with the Pluvial periods that the zoologists are primarily concerned. For this reason we should explain at the start what we mean by the term "Pluvial." We apply this name (capitalized) to the two or more stages, commonly assumed to be of late Pleistocene (Wisconsin) age, when the western basins were largely filled with lakes which have left definite records of their existence in the form of shore features, so well described by Russell (1883, 1885, 1889) and Gilbert (1875*a*, 1882, 1890). One reason for speaking of Pluvial instead of Quaternary lakes, and times, is that geologists are in disagreement as to the coverage and the desirability of the term Quaternary. We avoid the term Pleistocene for other reasons: (1) many of the waters may have lasted well into Postglacial time, (2) we have almost nothing to contribute to the timing of the ancient lakes, and (3) geologists are by no means in full agreement on these correlations. We apply the term "earlier pluvial" to former periods of humidity, so remote that the lakes then formed have left no clear-cut shore features. We employ the now rather commonly used term Postpluvial, when referring to the period of desiccation following the last high lake stage.

In naming the Pluvial lakes (Table I and accompanying outline of references) we precede the name of each, wherever feasible, by "Pluvial Lake," often dropping the word "Pluvial" in running discussions. This practice generally distinguishes these names at once from the names of Recent lakes, in which "Lake" ordinarily follows the specific name. We prefer to use the same name for successive Pluvial lakes in the same basin, as has been done in the classical examples of Lake Bonneville and Lake Lahontan. Thus we use "Pluvial Lake Chewaucan" for both stages of the lake which covered the modern Summer and Abert Lake basins in Oregon, and do not follow Allison (1946: 64), who named the earlier and deeper stage "pluvial Lake Chewaucan" and the later and shallower level "pluvial Winter Lake." In 1945 he used not only these names, but also "Ana Lake," for a very low intermediate stage. The successive fillings, concerning which there will often be doubts and diververge of opinion, are more satisfactorily designated as stages rather than as different lakes.

A few geologists have argued that climatic changes were not involved in the origin and desiccation of the Pluvial lakes. Thus Keyes, following a suggestion by Davis (1883), ascribed Lake Bonneville to orographic deformations. Keyes' view that Lake Bonneville must have been formed by the Snake River, and that it could not have been produced by an increased flow of the existing tributaries, is negated by the circumstance that numerous smaller basins, with very small drainage areas and certainly without a large inlet, were filled with deep lakes, apparently at the same time. On other grounds (pp. 31 and 100), Keyes' theory (1917–1918) fails to fit the facts.

Evidence on Time Relations

The geological timing, and eventually (if possible) the calendar dating, of the Pluvial periods in the Great Basin are problems of great concern to students of physiography, glacial geology, climatology, archeology, zoogeography, systematic botany, systematic zoology, and evolution. Correlation of the time data from these disciplines is a major purpose of the symposium of which this paper is a part. Similar correlations, but with little reference to the living biota, are involved in the symposium to which Cressman, Hansen, and Allison contributed (1946). If we can measure the time interval since the Great Basin was a well-watered land, we will be able to estimate the rate of physiographic changes, the length of Postglacial time, the time involved in major climatic changes, the period of human occupancy of western North America, the speed of dispersal and extirpation of plants and animals, and the rates of speciation.

Several geologists have been able to correlate epochs in the history of a few of the major Pluvial lakes with certain periods of montane glaciation (Russell, 1885, 1889; Gilbert, 1890; Upham, 1914; Hodge, 1930; Blackwelder, 1931, 1933, 1941, accompanying report; Blackwelder and Ellsworth, 1936; Allison, 1945; Antevs, 1945; Flint, 1947; Hansen, 1947). In a general way the periods of montane glaciation have been correlated by most geologists with the great ice advances of continental glaciation, and specific correlations are favored by some workers, particularly by Blackwelder. In his several contributions, Antevs (1925–1945) has even attempted the dating of the Pluvial lakes in terms of millenia. In their symposium papers published in 1946, Cressman, Hansen, and Allison have likewise estimated the duration of Postglacial events in terms of years as well as of climate. Huntington (1925) and Hansen (1947) have further contributed to the solution of this problem. Huntington has correlated the montane and continental glaciations, but has recognized some major disagreements in cycles and times. Jones (1914–1929), standing alone, advanced Pluvial Lake Lahontan into historic time. An opposite view was taken by Keyes (1917–1918), who claimed that Lake Bonneville "seems to have been well along toward complete desiccation before the Glacial epoch set in," and by Upham (1922), who confidently referred the first high level of the western lakes to the Nebraskan stage. Chiefly on the basis of mammalian fossil records, Hay (1927) dated Lake Lahontan from early Pleistocene. It is clear from these papers and from the summary discussions by Merriam (1918), Hay (1927), Daly (1934), Schultz (1937), Bryan (1941), Nolan (1943), and others, that there are major differences of opinion regarding the precise dating of the two or more high levels of the major Pluvial lakes. Discussions with outstanding Pleistocene geologists lead us to conclude that nowhere have any of the lacustrine or glacial phenomena of the Great Basin been synchronized with those of continental glaciation by concrete, undeniable physiographic evidence. The time correlations of the major Pluvial lakes have generally been made on a presumptive basis. The many small Pluvial lakes are correlated with the major ones on even less secure evidence. Recent researches by Hobbs (1943) and others have brought the probable limits of continental glaciation closer to the Great Basin, thus raising the hope that more definite time relations for the basin lakes may yet be determined.

From our examination of the shore lines of the Pluvial lakes, we agree with Blackwelder that there has been extremely little diastrophism or erosion in the Great Basin since the Pluvial periods. Occasional minor fault displacements slice across beach lines, and mountain gulleys cut through some lake terraces (for instance those on the east slope of Pluvial Lake Surprise), but no major physiographic changes seem to have taken place during Postpluvial time. Failure to recognize this circumstance appears to be the chief reason why Free (1914*a*) came to so many improbable conclusions regarding drainages in what he called the Lahontan period. Major diastrophic changes no doubt took place, however, during the very long "earlier pluvial" history of the Great Basin.

When the Pluvial period ended is a moot question. As mentioned above, Jones tried to insert the whole Pluvial history of Lake Lahontan into the historic time period. We would not go so far, but do feel convinced that within the last few thousand years there have been times when the desert was much better watered than it has been during the wettest years in the brief recorded history of the West. A main reason for this belief is the known long-period fluctuation in rainfall in various desert regions (Huntington, 1945: 529–572). Confirmation of this view is supplied by the evidence of Indian occupancy in regions of the West that are now too dry to support human life. It was perhaps during such Postglacial humid periods rather than during Pluvial times that man occupied regions now too dry to support the populations that existed. For this reason there are doubts regarding the correlation of Indian sites with Lake Bonneville (Harrington, 1934*b*), with Pluvial waters in the Mohave Desert (p. 86), Colorado Desert (p. 106) and Las Vegas Valley (p. 101), and with the supposedly Pluvial alluvial fan at Borax Lake, California (Harrington, 1939). We recognize, however, the impelling strength of evidence that man lived in the West during or immediately after the Pluvial period. It was possibly then that Indians carved the pictographs (Figs. 28–29) that we observed in the now arid parts of the course of Pluvial White River, Nevada (as in the very dry canyon 23 miles north of Hiko and at the mouth of Arrowhead Canyon). Preliminary examination of dried fish remains from Lovelock Cave (Loud and Harrington, 1929) and Humboldt Cave, in central Nevada, indicates that when these caves were occupied by early Indians, Humboldt Lake nearby was a permanent fresh-water lake (p. 41). Evidence for more or less recent moist periods can be found in the treatises by Antevs, Bryan, Campbell and Campbell, Cressman, Harrington, Huntington, and Jones (see Literature Cited). Some of the isolation and speciation that is dated from Pleistocene time may be much more recent. Now disconnected waters within many of the basins of western North America may have been connected and their fish fauna made uniform not many centuries ago. From a consideration of the evidences on climatic changes reviewed by Huntington it seems likely that such connections may have been established several times during the last three millenia. We believe, however, that most of the local differentiation and endemism among the fishes of the isolated desert waters dates from the end of the Glacial period. Hutchinson (1939) concluded that the similar differention of now isolated fish populations in Kashmir and Indian Tibet dates from the period of maximum glaciation.

The zoogeographic evidence as to the age of the Pluvial lakes of the Great Basin is far from convincing. In correlation with Postpluvial isolation, a limited degree of speciation has occurred here and there, but data are too meager to warrant any attempt to use the rate of species evolution in dating the Pluvial waters. We can only say that the available biological information is in harmony with the view that the Pluvial periods were of late Pleistocene time; it does argue against an early Pleistocene or Pliocene dating, but does not deny an early Postglacial correlation. A considerable body of observational and mathematical data indicates that small, closely inbreeding populations may speciate at a much more rapid rate than was previously thought possible (Wright, 1940*a–b*, 1942; Huxley, 1943). Biologists critically need time estimates of the Pluvial and Postpluvial history of the Great Basin, but have little to contribute to such dating.

Zoogeographical Evidence

Most recent students of desert animals correlate the distribution of the species that they study with the physiographic events that are commonly associated with the Glacial period. Thus Behle (1942) found that certain subspecies of horned larks seem to have originated in areas laid bare by the desiccation of lakes Bonneville and Lahontan. Hall and Dale (1939) stated that the range of a subspecies of kangroo rat "corresponds closely to the former outline of the Pleistocene Lake Bonneville." Linsdale (1938) mentioned "the boundaries of the old Lahontan Lake basin, which coincide closely with ranges of some geographic races of birds." Steven D. Durrant and David T. Jones (personal communications) are finding that the distribution of pocket gophers and molluscs, respectively, correlates finely with the Pluvial and Postpluvial history of Lake Bonneville.

Doubts have been raised as to whether Glacial events have been a controlling factor in determining the distribution of many forms of life in the western United States. The occurrence of similar, generally dark populations of small mammals on the isolated desert ranges, for example, has been attributed by Dice (1940) to parallel ecological adaptation rather than to Ice-age connections. Most birds and insects could have invaded the present isolated habitable areas as wanderers. Many invertebrates and plants can be dispersed through the air as eggs, spores or seeds. Despite such alternative explanations we may, with more or less assurance, correlate much of the distribution of all life in the Great Basin with events of the Pluvial periods.

The distribution of fishes provides what seems to be the least assailable data, by which we may line up the theoretical zoogeography of the Great Basin with the climatic and physiographic history of the area. Despite popular ideas to the contrary, there is no reliable evidence behind the assumption that fishes are commonly if ever dispersed via underground channels, and the only trace of tangible evidence that waterspouts or other wind phenomena transport fishes comes from tropical maritime regions in the paths of hurricanes and typhoons. The native fishes of the Great Basin appear to occur only in habitats which they have been able to reach through surface-water connections, by means of either active or passive migration. The dispersal of fishes is therefore closely linked with the history of the water courses (Hubbs, 1941*a*; Miller, 1946*a*).

Paleontological Evidence

Biological evidence on the climatic and hydrographic history of the Intermountain region would be much richer, if we had more than the present dribble of paleontological data on the fishes. The only reasonably well-known fossil fish faunas of the West are that of the Miocene Diatomaceous Shales, which is marine (David, 1943), and that of the Green River Eocene (Cope, 1884, etc.), which involves a fauna too early in fish evolution to be correlated closely with the distribution of Recent fishes.

Some fresh-water fossil fishes are known from beds in the Great Basin that are assigned to the Miocene, but these unfortunately are too few and too poorly known to furnish much help. They do tell us, however, that during the early stages of the present cycle of Great Basin geological history, types of fishes occurred here that are quite unlike those that now live in western North America. Thus from the "Amyzon Tertiary Beds" or "Amyzon Shales" of the Humboldt Valley, Nevada (presumably the beds referred by King, 1878, to the Green River Eocene, and named the Miocene Humboldt Formation by Sharp, 1939*a*), Cope (1871, 1872, 1879*a*, 1884) described two fossil fishes, *Amyzon mentalis,* a catostomid of a type found fossil also in Colorado and British Columbia and living in eastern North America, northeastern Middle America and China, and *Trichophanes hians,* a member of the Aphredoderidae, extant only in eastern North America. A cyprinid which appears on original study to be more closely related to Recent forms of the Great Basin was collected by Percy Train in the Virgin River beds, regarded by Merriam (1910, 1911) as of Miocene age.

Pliocene fish fossils are no more illuminating. The supposedly Lower Pliocene Esmeralda Formation, however, has yielded a sucker and a minnow, as mentioned on p. 46. The minnow of this Formation, *"Leuciscus" turneri,* is shown by its slender form and large, strongly forked caudal fin to be an open water, lacustrine type.

Fish remains from the Pleistocene should be of utmost significance in elucidating the history of the Great Basin and its life, but most of them are fragmentary and few have been carefully studied and critically compared with Recent species. Far-reaching suggestions, however, may be drawn from two fossil species which have been described (Jordan, 1907, 1908; Hay, 1907; Eastman, 1917) from the beds which are consistently interpreted as having been laid down by Pluvial Lake Lahontan and which have been tied in with moraines (Russell, 1885). These are a stickleback, *Gasterosteus doryssus* (first misplaced in the Atherinidae), and a killifish, *Fundulus nevadensis* (referred by Eastman for no apparent reason to a new genus, *Parafundulus*). A third species, identified by Jordan (1924) as the Recent Great Basin form, *Cottus beldingii,* is not of critical significance (an examination of Jordan's material indicates that his count of 20 caudal vertebrae is correct or nearly so and that therefore the fossil form is not referable to the coastwise types with a markedly increased number of vertebrae). *Gasterosteus* and *Fundulus* are both coastal fishes, living in bays and in the lowland portions of streams. These fish fossils tell us that the waters of the Lahontan Basin must have had a genetic connection with waters that once reached the Pacific Ocean. An outlet to the sea from Lake Lahontan, at the present elevation of the Great Basin, presumably would not have sufficed to bring in *Gasterosteus* and *Fundulus,* for it is not to be expected that these lowland genera ascended the mountain streams to the high rim of the lake. The recent discovery (Miller, 1945*c*) of other fossil species of *Fundulus,* two in the Death Valley basin and one in the Mohave Desert, suggests that the lowland connection may have been from the southwest, where this genus is known both living and fossil and where *Gasterosteus* now occurs. It seems to us probable that these genera reached what is now Nevada when that area was coastal lowland, presumably prior to the elevation of the Sierra Nevada. This interpretation calls for a recent elevation of the Great Basin as well as of the Sierras and may be opposed by geologists. Blackwelder (1934: 561–562), however, has suggested that a general uplift, or series of uplifts, took place in the central Rocky Mountain region during Pleistocene time, resulting in the origin of the Colorado River as a continuous stream system. Thus the theory that a very large area was elevated during the Pleistocene would nicely explain the rapid erosion of the canyons of the Colorado River, which Blackwelder and others think may have been confined to Quaternary time.

The time when *Fundulus* and *Gasterosteus* invaded Nevada calls for consideration. It may be assumed that they arrived after the ancient, warm Eocene period, for they are Recent genera and are not tropical (*Gasterosteus* is subarctic and temperate, and *Fundulus* is temperate). The incursion probably dates from Miocene, Pliocene or early Pleistocene time.

It is quite possible that the particular beds that contain *Fundulus* and *Gasterosteus* are older than the lake deposits which have been correlated with montane glaciation. The beds of the lakes may represent many geological times (see below). The coastwise fishes may first have inhabited an "earlier pluvial" stage of Lake Lahontan, or an antecedent lake in the same area. It will be recalled that Merriam (1918) and Hay (1927) dated mammalian fossils from Lahontan beds as early Pleistocene.

The former occurrence of these coastwise genera, and of the peculiar sucker *Chasmistes cujus* in Pyramid Lake (Snyder, 1914, 1917*a*: 40), negates the claim of Russell that the Lahontan basin was completely arid before it became filled with water. *Gasterosteus* and *Fundulus* no longer persist in Nevada; they may have been extirpated during an inter-Pluvial period of great aridity. We can not subscribe, however, to Russell's belief that the Lahontan waters completely disappeared between the two main high-water periods of Lake Lahontan. Enough spring and creek water must have remained on the parched land surfaces to have maintained the fish fauna which has persisted to the present in this entirely enclosed basin. The persistence of the Lake LeConte snail *Hydrobia* (p. 105) in Dos Palmas Springs is pertinent to this interpretation.

The paleontological information on other groups of animals and the fossil plant records may bear more definitely on the age of the Pluvial lakes, but we do not feel competent to evaluate such data.

Correlation of Physiographic and Ichthyological Evidence

In the present stage of knowledge it would verge on fiction to attempt to hypothesize in any detail the pre-Pleistocene history of the faunas of the Great Basin. Alternating periods of floods and desiccation, of lava flows and stream capture, of mountain building and planation, of speciation and extinction, must all have modified the distribution of life, in ways that we cannot now analyze in any detail or with any assurance.

Hundreds of lakes have come and gone throughout the arid portion of the western United States. Over a long period of time—Miocene, Pliocene, and the many millenia of early and middle Pleistocene—lakes formed, filled their depressions with deposits and disappeared. Through most of the Great Basin and in large adjoining portions now drained by the Columbia and Colorado rivers, lacustrine deposits form one of the most conspicuous elements in the western landscape, vying for attention with the upturned fault blocks and intervening basins, with the lava flows, and with the alluvial fans and bolson fills. Generally these lake deposits lie behind lava cross-barriers, most of which were cut through by the overflowing lake so that the lacustrine beds have now become extensively dissected. The major basins like those of Lake Bonneville and Lake Lahontan must have been occupied by lakes of "earlier pluvial" periods—probably by a long sequence of such impoundments. Since shore-line features of these very ancient lakes have been effaced by time, the history of these waters will have to be traced from studies of the alluvial deposits that fill their basins to enormous depths (Russell, 1896; Lee, 1908: 68–69; Jones, 1929; Eardley, 1938; Pack, 1939, etc.). Diastrophic movements of various sorts no doubt modified the history of these earlier lakes so greatly as to complicate or even obscure the record of their existence.

We reach firm ground only when we approach the present. Not until then does the palehydrographic picture become clear enough to provide us with what might be called the family trees of the springs and creeks and lakes of the present. It is only with the Pluvial and Postpluvial events that we may safely venture to correlate our knowledge of Recent fish distribution in the Great Basin.

The present distribution of fishes in the remnant waters of the Great Basin is to a large degree explained by the recent geological history of the region, and in turn our knowledge of the fish distribution helps to test the conclusions of the physiographers. The evolutionary relationships and history of many of the fishes can be outlined with some assurance when we have, as we often do, some clear-cut evidence on the past connections and disruptions of the waters which they inhabit. Conversely, when we discover closely related fishes in a chain of now separated springs or creeks, we supply evidence that these isolated waters are relicts of a once wide-spread and integrated stream system; and when we find adjacent basins with dissimilar fish faunas, we furnish an indication that the waters of these basins have not been interconnected within recent geological time (Snyder, 1913, 1914, 1917*a*; Hubbs, 1941*a*; Hubbs and Miller, 1943; Miller, 1943*b*, 1946*a*, in press). As is often true when two disciplines are brought to bear on one focus, the support is mutual.

The interior drainage of the Great Basin is surrounded by the stream systems which harbor the four main fresh-water fish faunas of the Pacific drainage of North America (north of Mexico). To the north lies the vast area of the Columbia River basin, of which the part of the Snake River system that lies above the great falls is historically and faunally allied to the Bonneville division of the Great Basin. On the eastern side, across sharp mountain divides, are the deeply entrenched waters of the Colorado River system. On the south, in the extension of the Basin-and-Range physiographic province, there is a very indefinite separation between the Great Basin and the Colorado system (Free, 1914*a*). The interior drainage is sharply cut off from the coast by the Sacramento and Klamath basins, each of which, like the Colorado and the Columbia, has a distinctive and no doubt ancient fauna (Miller, 1946*b*). The Klamath fauna is essentially of Great Basin affinities, for this basin (see p. 68) probably did not overflow until it became filled with Pluvial waters.

The fishes of the Great Basin exhibit some relationship with those of each of the surrounding faunas, though the endemic genera of the Colorado, Sacramento and Columbia systems are lacking (except where, or if, we include in the interior drainage the now more or less disconnected streams which in Pluvial times flowed into the Sacramento, Columbia, and Colorado). The types which are common to the interior and exterior drainages are mostly of mountain-creek groups (*Salmo, Prosopium, Catostomus, Pantosteus, Rhinichthys,* etc.), which may well have been transferred from system to system by such means as (1) stream captures, (2) headwater distributary connections like that of Two-Ocean Pass (Evermann, 1892), and (3) the migration of creeks back and forth over alluvial cones that lie across such low divides as that between Coyote Creek and Pajaro River in California (Branner, 1907; Snyder, 1913). Many connections of these types were no doubt effected during a period of accelerated stream flow and raised lake levels.

The fishes of the Great Basin do not comprise a zoogeographical unit, but rather a complex of more or less unrelated faunas. The larger of the separate hydrographic basins have moderately rich fish faunas, but most of the smaller separate basins that are not entirely fishless harbor only 1 to 3 species. Dozens of other enclosed basins, now without any native fishes, may well have contained fish life at some past time. We are inclined to accept the views of Russell (1896) that, in harmony with the early opinion of Gilbert (1875*a*), here is probably not an enclosed basin in the State [of Nevada] but what had is lake during Pleistocene times," and of Meinzer (1922) that every dry lake ed was probably once covered with at least a shallow lake.

The enclosed Basin-and-Range type of topography extends not only into he California deserts but also, under the sea, far to the westward of the outhern California coast (Shepard and Emery, 1941).

1.—LAKE BONNEVILLE SYSTEM

The largest of the interior drainages, covering most of central and northwestern Utah, is named the Bonneville, from the immense Pluvial sea (map 1, no. 1[3]) of which Great Salt Lake is a remnant. In correlation with the size of the basin, the Bonneville has the most extensive of the interior-drainage fish faunas of the West, in terms of genera and species. According to our present provisional estimates, the Bonneville fishes (including the species of the related fauna of the Upper Snake River) comprise 5 families, 12 genera (2 endemic), 22 species and at least 28 kinds counting subspecies (of these, 3 species and a total of 4 forms, are known from the Upper Snake fauna but not from the Bonneville proper). Field work of 1942 suggests that several more subspecies will eventually be recognized. Treatises on the Bonneville fish fauna, in addition to those cited in the following discussion, include: Cope (1874), Cope and Yarrow (1875), Jordan and Gilbert (1881), Jordan 1891*a*), Snyder (1924) and Tanner (1936).

Many of the outlying portions of this Pluvial drainage basin, particularly those near the Nevada border of Utah, are now isolated as separate minor drainages. The fish fauna in each fragment clearly tells the story of the Pluvial connections, despite the fact that confusion as to the hydrographic relations of these minor valleys has been indicated (Jones, 1940; see also page 66). One who has studied the desert faunas could, if lost, determine by taking a fish sample whether he was in a stream that once flowed into Lake Bonneville. We have recently determined that Snake Valley and Deep Creek, tributary in flood to the Great Salt Lake Desert south of Wendover, near the Nevada–Utah line, possess a rather rich fish fauna (8 genera and at least 10 kinds), of a composition which demonstrates that the great salt wastes in former times must have been covered with fresh waters. Similarly, in sampling the fish of Thousand Spring Creek of Nevada and Utah in 1934, before knowing its former connections, the Hubbs family determined from the fishes collected that the stream was once tributary to Lake Bonneville, and they then traced the stream bed down until it dipped below the higher terraces of the ancient lake.

The limited endemism exhibited by Bonneville fishes (2 out of 12 genera, 14 out of 22 species) indicates that connections with one or more adjacent faunas once existed, and at no greatly remote geological date—perhaps in the Pliocene. Connections with the Colorado seem to have been restricted to a few headwater transfers. It seems almost certain that some such headwater connections have existed. In at least four places a faunal transfer across low divides must be taking place now, as a result of the diversion of creeks for irrigation. One such transfer, described to us by A. M. Woodbury and recorded by LaRue (1916: 149–150), carries water from the head of Santa Clara River, in Grass Valley, Washington County, southwestern Utah, through a tunnel over the divide into Pinto Creek, of the Great Basin. Fish, no doubt, are thus being transported from the Colorado system into the Bonneville basin. A transfer in the reverse direction has been going on since about 1895, through Tropic Ditch, by which part of the water of the East Fork of the Sevier River is led along contours into the headwaters of Paria River, a tributary of the Colorado near Bryce Canyon, Utah. Transfer of water, and presumably of fish life, has taken place since 1913 from Strawberry Reservoir, on a tributary of the Colorado River in Wasatch County, Utah, by way of a tunnel through the mountains into Diamond Creek, Utah County, a Great Basin stream. Ditches also divert water across Daniels Pass, northwest of Strawberry Reservoir, from the Colorado basin into Daniels Creek, a tributary of Provo River of the Great Basin (LaRue, 1916: 146–147, pls. 13–14). A Pluvial headwater transfer probably occurred in both directions near Kanarraville, in southern Utah, where a large alluvial cone straddles the Bonneville–Colorado divide. The stream on this divide is diverted to both sides for irrigation, and in periods of ampler flow no doubt wandered back and forth across the divide to carry the fish first into one system and then into the other. By this connection, and probably by other similar transfers, such fish as *Pantosteus* and *Rhinichthys osculus* could have gotten into the Bonneville basin.

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[3] The same numbering system of the Pluvial waters is employed on the map, through the text, and in the table (pp. 148–155) and references (pp. 156–165) dealing with these waters.

Considerable subspeciation within the basin is in harmony with the assumption of geologists that the Bonneville waters have been greatly diminished and much disrupted since late Pleistocene. It cannot be categorically stated, however, that all such differentiation has occurred since the desiccation of Lake Bonneville. Some of the Recent ecotypes may have been differentiated in Pluvial times, and if so, they attained their present distribution merely by habitat selection, rather than by rapid and recent speciation. Some of the local differentiation, especially in Bear Lake, is in the nature of modifications to meet lacustrine conditions.

Snake River Division

In his grand memoir on Lake Bonneville, Gilbert (1890) dramatically demonstrated that the waters of this inland sea rose until they found an outlet into the upper Snake, a Columbia River tributary. Ichthyologists then confirmed this interpretation by discovering that several elements of the Lake Bonneville fish fauna occur in the upper Snake (Jordan, 1891*b*; Evermann, 1892; Gilbert and Evermann, 1894). The combined fauna lacks the endemic genera of the Columbia and the semimarine types (lampreys, sturgeons, salmon, etc.), all of which are stopped by the higher falls of the Snake. The only plausible theory that will explain why at least some of these types have not persisted above the falls, seems to be that the fauna of the upper river came to some cataclysmic destruction, during or after the formation of the falls and prior to the Bonneville overflow. The great and relatively recent lava flows (Russell, 1902; Stearns, Crandall and Steward, 1938) presumably constituted such a cataclysm, for it may be assumed that the flows killed all the fish in the main water courses by overheating or poisoning the water, or by temporarily eliminating the streams. Such an explanation may also account for the absence of native fish life from the Mono basin of eastern California (see p. 79). Jordan (1891*b*) similarly explained the lack of fishes in the Yellowstone River system above the great falls on the assumption that the lava flow which formed the plateau of Yellowstone National Park destroyed the fish life which had previously existed there, but it seems more probable that the lack of fish in the Yellowstone Lake region is attributable to the almost omplete filling of the lake basin by Glacial ice (Howard, 1937). In agreement with the geological evidence that some of the cold upper tributaries of the Snake lay above the lava flows and hence escaped destruction, there occur in the upper Snake certain headwater types (three suckers, *Catostomus catostomus pocatello, Catostomus syncheilus* and *Pantosteus jordani,* and one sculpin, *Cottus bairdii tubulatus*) that also inhabit other parts of the Columbia River system but are absent from the Bonneville basin proper. The isolated fauna of the Lost River group of streams (p.76) seems to represent a partial relict of the upper Snake fauna as it existed prior to the lava flows. The Wood River fauna (p. 77), a curious mixture, contains one Bonneville type (*Snyderichthys copei*), despite the fact that Big Wood River enters the Snake below the major falls. It would not be plausible to time the connection of Lake Bonneville with the Snake as older than the Pleistocene, for two reasons: (1) the outlet-level terraces are still very little eroded; (2) none of the fish species that exist on the two sides of the now dry outlet channel is known to have undergone differentiation as a result of this disruption of the range. No definite dating of any of the Lake Bonneville levels can be regarded as well established. Harrington (1934*b* and personal communication) believes that the lake may have persisted even into the period of the early human occupancy of the region, but the supporting data for this view are still tenuous.

From the zoogeographical evidence there is no clear way of determining whether, during the short period of overflow, the Bonneville fishes moved south from the Snake into the Bonneville basin proper, or north into the Snake. Likely some went each way. *Richardsonius balteatus hydrophlox* almost surely made the trip southward, for it occurs above barriers in various parts of the Columbia River system. *Rhinichthys cataractae* very probably moved the same way, for on the Pacific slope it is otherwise known only in the Columbia fauna. That *Snyderichthys* (Miller, 1945*a*) may have gone the same way is suggested by its occurrence, just mentioned, in the Wood River system. *Pantosteus, Catostomus,* several cyprinids in addition to the three mentioned above, *Cottus,* and other genera may well have dispersed in the same direction, or may have moved both ways. Other fishes probably antedate, as Bonneville residents, the time when the lake temporarily overflowed. One of the two endemic genera (a cyprinid, *Iotichthys*) and the Utah Lake sucker (*Chasmistes liorus*) are unknown in the Snake system and very probably existed in the Bonneville basin before the time of discharge. The peaknose cisco (*Leucichthys gemmifer* Snyder), a subartic relict confined to Bear Lake, is a zoogeographical enigma.

Some but not all of the fish-distributional evidence might be cited to support the aberrant theory of Keyes (1917–1918). He claimed that Snake River was formerly the headwaters of "Old Virgin River," which flowed through the Bonneville basin and the Muddy River to join the Colorado. The similarity of the Snake and Bonneville faunas could thus be explained, but the failure of this common fauna to reappear in the Virgin River and in the remnants of Pluvial White River (p. 96), which would have been the main lower tributaries of the ancient through-flowing master stream, argues very strongly against this theory. Any outlet from Lake Bonneville to the southward must have been much older than the last connection between the Bonneville and upper Snake waters. Keyes' argument that Lake Bonneville could not have formed with its main inlet (Bear River) entering so close to its outlet is negated by the same drainage relations that existed in Pluvial times and persist to the present in Bear Lake, which is fed by the same river.

Tributary Pluvial Lakes

Bear Lake (1*a*)[4], in Utah and Idaho, was the largest of the few Pluvial lakes that were tributary to Lake Bonneville. It was not treated by Gilbert (1890), nor was it indicated on Meinzer's (1922) map of Pleistocene lakes, although the present Bear Lake was indicated by Hayden (1872: 156) and by Peale (1879: 587–589) as the remnant of a former, larger body of water. Peale suggested that Bear Lake Valley was occupied by three lakes, respectively, Pliocene, Early Quaternary and Late Quaternary. Bear Lake has only recently been described in detail as a Quaternary lake (Mansfield, 1927: 30–32, 204–205; Richardson, 1941: 5, 35). The discharge of Bear Lake still reaches Great Salt Lake by way of Bear River. The fishes of Bear Lake are definitely part of the Bonneville fauna, although, as already noted, they include some local differentiates that are somewhat modified for lacustrine life; also the enigmatic *Leucichthys* and two other endemic corregonines (Snyder, 1919).

Little Salt Lake (1*b*), in Iron County, southern Utah, presumably had a higher Pluvial level and is thought to have discharged through Hieroglyph Canyon into the Escalante Desert arm of Lake Bonneville (Meinzer, 1911*b*). The occurrence in this lake of an endemic Bonneville type, *Iotichthys phlegethontis* (reported by Tanner, 1936), confirms this interpretation. Meinzer did not include the lake on his 1922 map, but Jones (1940) did chart it.

Jones (1940) treated Pine Lake (1*c*) in southwestern Utah as a Pluvial lake. It lay between 38° and 39° N. Lat., just off map 1. It was in Sage Brush Valley, which was shown by Gilbert (1890) as a trough connecting the Snake Valley and the Escalante Desert arms of Lake Bonneville. Whether there was a connection between Pine Lake and Snake Bay is apparently undetermined, and we have no fish data to bring to bear on the problem. Several small lakes and playas, near the southern boundary of the Bonneville drainage basin, may have been lakes in Pluvial times.

Several small mountain lakes in the Bonneville and in the Colorado systems were mapped by Jones (1940) as Pluvial waters, without citation of evidence as to their age or as to whether their basins were filled with Glacial ice. There is no significant fish-faunal data on these mountain lakes, and they hardly enter into our problem.

2–15.—LAKE LAHONTAN SYSTEM

Next largest of the interior drainages and, in interesting correlation, second only to that of Lake Bonneville in the number and variety of its fishes, is the basin of Lake Lahontan (map 1, no. 2). "Lake La Hontan," merely named by Hague (1877*c*: 818), was treated in more detail by King (1878) and classically monographed by Russell (1885). This lake bed occupies much of Nevada, some adjacent parts of California and a few square miles in Oregon. Our present estimate of the native fish fauna of the Lahontan, agreeing closely with that of Snyder (1917*a*), is as follows: 5 families (same as in the Bonneville), 10 genera (only 2 fewer than in the Bonneville), 13 species (as contrasted with 22). Including subspecies as now separated (some very provisionally), the Lahontan fauna is perhaps richest. It comprises, we estimate, about 30 forms, as compared with perhaps 28 in the Bonneville and about 24 the Death Valley system. The relatively high number of total forms is correlated with the isolation of local populations, for the Lahontan system has become greatly disrupted since Pluvial times (Russell, 1885; Free, 1914*a*) and several of the adjacent lake-containing valleys attained a temporary connection with Lake Lahontan during one or more high lake levels. In contrast with Lake Lahontan, Lake Bonneville filled a much larger proportion of its drainage basin and had few tributary lakes. The composition of the fish fauna of the Honey Lake Basin, in Lassen County, California, fully confirms the hydrographic evidence that Honey Lake was flooded by a western arm of Lake Lahontan (Russell, 1885; Snyder, 1917*a*; Guernsey, Koeber, Zinn and Eckmann, 1919; also original observations).

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[4] Numbers followed by lower-case letters are used for Pluvial waters that are beyond the limits of map 1. These numbers are included in the table (pp. 148–155) and references (pp. 156–165) dealing with these waters.

3–15.—**Pluvial Lakes Connected with Central Lahontan Basin**

Many valleys were connected by surface waters with the Lahontan system for either a long or a short portion of the last wet periods, but are now completely isolated by intervening divides, or are connected only by flood waters (which seem rather ineffectual from the standpoint of faunal connections). There are two main groups of these disrupted valleys. One group lies to the south and east of the Reese River, Nevada, which in itself is becoming fragmented (Waring, 1918). The other group lies to the northwest, from the Honey Lake and Eagle Lake regions of northeastern California to the Lahontan lake flats (Smoke Creek Desert, Granite Creek Desert and Black Rock Desert) in northwestern Nevada. The common factor in the isolation of the basins is desiccation, which has eliminated the lower channels of stream systems and has lowered the lake or bay surfaces to below the level of the outlet rim. Other factors which have contributed to the disruption of some basins include the formation of barriers of lava and of alluvium. The fish life in these isolated waters is all theoretically derivable, and in some of the valleys is not at all differentiated, from the kinds that have occupied the central part of the Lahontan system. The ichthyological data bearing on the former hydrographic integrity of the whole Lahontan system, in so far as it was known at the time, was very well summarized by Snyder (1914, 1917*a*).

The harmony of the physiographic and ichthyological data is exemplified by our discoveries in the now isolated valleys lying between the southern extension of the Ruby Range and the Reese River, in central Nevada. We therefore present this evidence first.

3.—Lake Newark and Fish Creek.—Years ago Free (1914*a*) stated that Little Smoky and "Gibson" (Newark) valleys (lying just southeast of Diamond Valley, next to be discussed) were part of the Lahontan watershed, but he gave no specific evidence to support his belief. We are now able to supply such evidence. Little Smoky Valley has a continuous arroyo or flood-water connection with Newark Valley (formerly called White Pine Valley). Thirty odd years ago, according to local testimony, the waters of Fish Creek in Little Smoky Valley were diverted by slight ditching into Newark Valley. That sump basin contained what may be called *Pluvial Lake Newark,* the uppermost terrace of which we followed in 1934 to and across the low divide between Newark Valley and the South Fork of Humboldt River. It is thus clear from the physiographic evidence (which was not recognized by Russell) that these two valleys east of Eureka were, for a brief time at least, parts of the Pluvial Lahontan drainage. The fish data are in agreement with the physiographic evidence: Fish Creek is populated by a local subspecies of the chub *Siphateles obesus*, and springs which form the remnants of Pluvial Lake

Newark are inhabited by a closely similar form of the same species, which is common in the Lahontan system. The differentiation of the Fish Creek and Newark Valley chubs presumably accompanied the Postpluvial desiccation. We found no evidence to substantiate Spurr's suggestion (1903) that a Pleistocene lake probably covered the greater part of Little Smoky and White Pine (=Newark) valleys. If such a lake existed, it was presumably of an "earlier pluvial" period.

4.—Lake Diamond.—Diamond Valley, located about but mostly north of Eureka, Nevada, is the site of the rather large Pluvial Lake Diamond. The uppermost terraces (Fig. 10) of this body of water were found by altimeter readings to lie at the same altitude as the summit of Railroad Canyon (Fig.

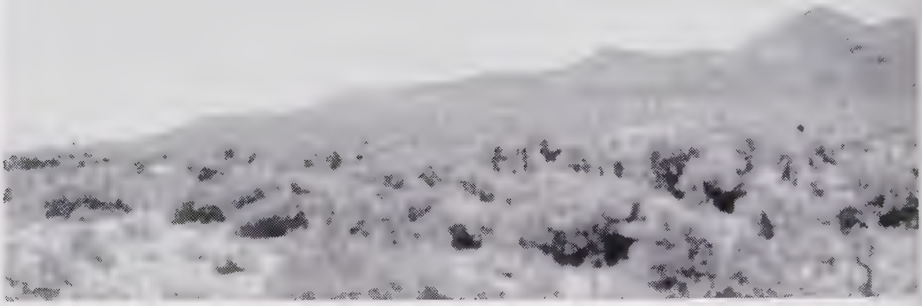

Fig. 10. Terraces representing the western shoreline of Pluvial Lake Diamond, near Eureka, Nevada. The highest and strongest terrace represents the outlet level (Fig. 11).

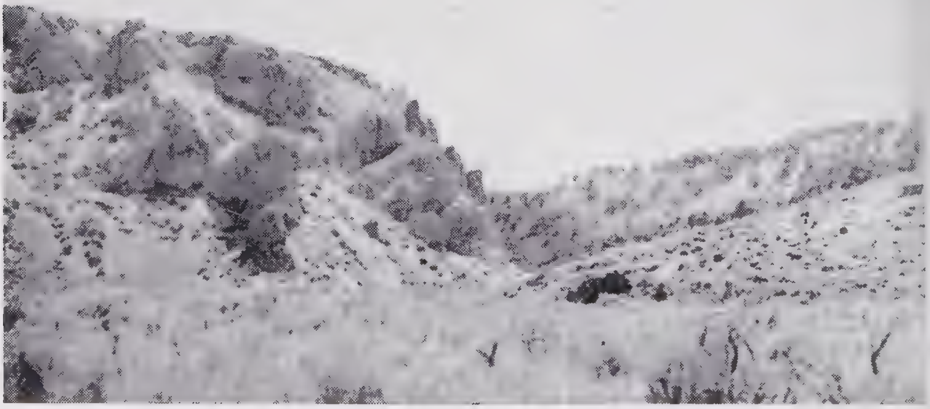

Fig. 11. Railroad Canyon, the outlet of Pluvial Lake Diamond, at the same elevation as the highest of the lake terraces (Fig. 10).

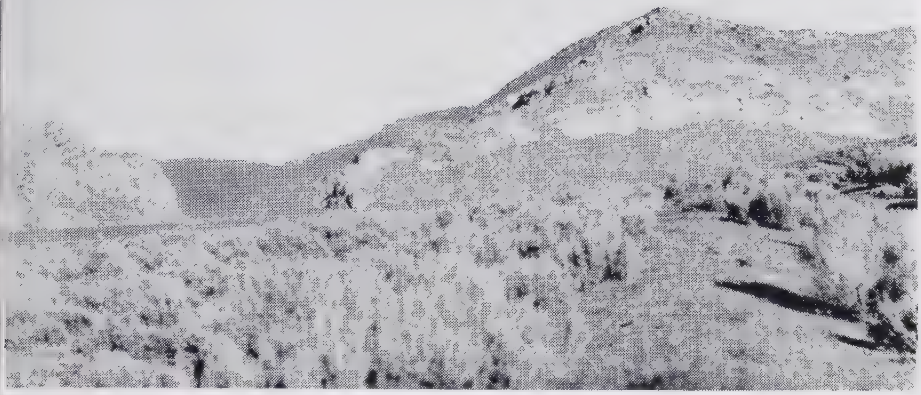

Fig. 12. Devils Gate, near Eureka, Nevada, formed by the main tributary of Pluvial Lake Diamond. A large area to the westward once drained through this channel.

11), by which the ancient waters obviously drained into the South Fork of the Humboldt River (Hubbs, 1941*a*; conflicting statements regarding the discharge were given by Free, 1914*a*); the outlet is misplaced on the lake maps by Meinzer, 1922, and others. At present the springs in Diamond Valley contain a distinct form of *Siphateles obesus* and a dace (*Rhinichthys*, subgenus *Apocope*) that is hardly different from the Lahontan subspecies.

Allocating Lake Diamond with the Lahontan system brings in several valleys to the westward (Free, 1914*a*). Field examination clearly shows that these valleys drained along the course of still existing arroyo channels through Devils Gate (Fig. 12) into Diamond Valley. Two of the valleys, one northern and one southern, each contains, in an isolated spring, a form of the subgenus *Apocope* that is only slightly differentiated from the Lahontan subspecies. These basins Russell correctly mapped as parts of the maximum drainage area of Lake Lahontan. Pleistocene (probably "earlier pluvial") lake beds have been identified in Kobeh Valley above Devils Gate (Merriam and Anderson, 1942). The correlated hydrographic and ichthyological data just cited have already been mentioned briefly (Hubbs, 1941*a*).

5–7.—LAKE GILBERT AND LAKES IN CRESCENT AND CARICO VALLEYS.—A basin on the west side of Simpson Park Range, located northeast of Austin, Nevada, probably also had a brief Pluvial connection with Humboldt River. This basin comprises Grass Valley proper as well as a larger, nearly dry depression just to the northward. Free (1914*a*) claimed that Grass Valley, as well as Crescent Valley to the northward, discharged into Humboldt River, but he presented no data to support this view. We made field observations in 1938 that do confirm this idea. The fish springs in Grass Valley are in a water course that leads northward toward the bed of an ancient lake (map 1, no. 5), for which we propose the name of *Pluvial Lake Gilbert*, in memory of Grove Karl Gilbert's classical contributions to Great Basin hydrography. Lake Gilbert lay in Townships 21 to 26 N., Ranges 46 to 48 E., between Grass Valley proper and Crescent Valley. It has been roughly mapped since the time of Russell (1885), but Free (1914*a*) found no evidence for a long concentration of drainage. Its area probably exceeded 100 square miles. Near its center there remains a dry lake about 3 × 13 miles in major dimensions, largely surrounded by dunes. At about mid-depth of the ancient waters, near Walti Hot Springs, there are sharply marked lake terraces, and, up to 100 feet higher, fairly definite wave-cut terraces slice horizontally across the draws and alluvial cones. Altimeter readings taken on the highest point of a probably lacustrine clay flat that separates the north end of Lake Gilbert basin from Cortez (Tenabo) Canyon (see U. S. G. S. Cortez Quadrangle) were only 10 feet higher than the reading on the highest terrace. It seems virtually certain, therefore, that at least temporarily this lake had an outlet through the now dry and precipitous canyon into Crescent Valley (map 1, no. 6). This valley in turn drained, and, as we learned locally, in high floods still discharges, into Humboldt River. Thus Grass Valley is added with some assurance to the probable limits of the Lake Lahontan drainage at the height of the Pluvial period.

The fish evidence again ties in nicely with the physiographic data. The only fish that we found in the Crescent Valley drainage is a kind of dace (*Rhinichthys osculus*) that seems to be inseparable from the Lahontan subspecies. This would be expected, since Crescent Valley still has an intermittent junction with the Humboldt River (immediately north). But since Grass Valley had only a temporary and long since abandoned connection with the Humboldt, one might expect any fish in its basin to be differentiated. That is what we did find, for the only species that we collected in the Grass Valley spring is a very distinct, new dace (*Rhinichthys*), perhaps specifically separable from *R. osculus*. Obviously as the result of parallel speciation, it approaches the peculiar minnows that live in the valleys between the Lahontan and Bonneville basins (pp. 51–57). The steepness of the outlet no doubt precluded the invasion of Lake Gilbert by most of the Lahontan fauna.

Carico (or Caraco) Valley (map 1, no. 7), lying northwest of the Lake Gilbert basin, is indicated by seemingly reliable local testimony to be devoid of native fish life. We discount several local claims that "native" trout occur in the semipermanent streams that are tributary to Carico Dry Lake, but we did not explore the basin. The present lake bed, now usually bone-dry, was said by Hague (1877*a*) to discharge in flood stages through Rocky Pass into Crescent Valley and thence into Humboldt River.

Hague (1877*a*) discussed evidences for the existence of an ancient lake that may have extended from the northern part of Carico Valley, where the playa remains, over the low pass into Crescent Valley. A "Glacial-Period" lake in this location was mapped by King (1878), who also charted a lake of this type in the main part of Crescent Valley, where there are now shallow playas that occasionally overflow into Humboldt River. Quaternary lakes in these localities have not been recognized by Russell (1885), Gilbert (1890) or Meinzer (1922). If lakes of any size or importance formed here during Pleistocene time, they probably existed in "earlier pluvial" periods.

8–9.—BUFFALO LAKE AND LAKE IN ANTELOPE VALLEY.—A basin in north-central Nevada shows very clearly the shore features of a sizeable though shallow Pluvial lake (map 1, no. 8), which was mapped by Russell in 1885. *Pluvial Buffalo Lake,* as it may be called, probably discharged eastward into the lower Reese River, for the narrow intervening divide is very low (see Sonoma Range Quadrangle). Russell (1885) and Free (1914*a*) both included the valley in the maximum drainage basin of Lake Lahontan. Waring (1918) thought that the basin might still discharge into Reese River in exceptionally wet seasons, but he noticed no outlet channel. Our field observations lead us to think that the basin is now perennially enclosed, for the flood-water course from the divide is toward the playa. Precise levelling would be required to determine if the highest terrace is as high as the plain between the lake bed and the river. Emphatic local testimony indicated that the basin supports no fishes. None were found, but two of the springs (Buffalo and Kane) were not visited.

Opening into the west side of Reese River Valley farther south, Antelope Valley contains a dry lake (map 1, no. 9), which is said to discharge at times into the river (Waring, 1918). Like other parts of the Reese River drainage basin, Antelope Valley contains Tertiary lake beds, but except for the present small playa no indications of a Pluvial lake have been given. A local resident stated that Antelope Spring, the only permanent water of consequence in this valley is a "mud hole without any fish."

10.—LAKE WASHOE.—The present remnants of this lake (Russell, 1885) still discharge into Truckee River and contain the typical Lahontan chubs (Snyder, 1917*a*, and personal observation). Two other lakes (11 A–B) were tributary to Lake Lahontan through Truckee River.

11A.—LAKE TAHOE.—It seems probable that this high lake, now tributary to Pyramid Lake, existed during at least part of Pluvial time as well as throughout Recent time (Russell, 1885; Lindgren, 1898; Davis, 1933). Meinzer (1922), however, did not include Tahoe among the Pleistocene lakes of the Basin-and-Range Province. LeConte (1883–84) theorized that the very deep basin was entirely filled with Glacial ice. Russell (1883: 204) said it was surrounded by glaciers. Lake Tahoe supports a typical Lahontan fish fauna (Snyder, 1917*a*). The occurrence in Lake Tahoe of the lacustrine Lahontan chub, *Siphateles obesus pectinifer,* and of a lacustrine trout, *Salmo regalis,* related to *S. smaragdus* of Pyramid Lake, suggests that Lake Tahoe may have been elevated to its present level, far above Lake Lahontan, subsequent to the origin of the Lahontan fauna.

11B.—LAKE TRUCKEE.—Lindgren (1898) described a temporary Glacial lake in the course of Truckee River, the outlet of Lake Tahoe. This is shown on map 1 just north of Lake Tahoe (no. 11A). Lake Truckee, to formalize the name of "the Truckee lake," was dammed by a lava flow. It is believed to have drained itself by the down-cutting of its outlet during the later part of the Glacial period. Many lakes that are still extant and many others that have disappeared were produced in the Sierras during Pluvial times by moraines, lava flows and alluvial fans. Earlier lakes were also produced—for instance those on the course of Feather River in Mohawk Valley, California (Turner, 1891).

12.—EAGLE LAKE.—This lake, lying northwest of Honey Lake, was indicated by Russell (1885), Snyder (1917*a*) and others to be a part of the Lahontan system, because they thought that it discharges into the Honey Lake basin by seepage through an alluvial barrier. This idea now appears to be erroneous (Grinnell, Dixon, and Linsdale, 1930). Free (1914*a*) stated that the waters of Eagle Lake "do not now reach the central basin, but they did so very recently." On this point our observations lead us to agree, though not very confidently, with Free. Altimeter readings indicated that the highest well-defined terrace stands 50 feet above the present lake level. What appeared to be a beach pebble was found 10 feet higher and a possible terrace was seen 30 feet higher. The highest level probably produced a surface discharge, but we cannot be sure, as we do not have the exact elevation of the lowest point in the surrounding rim. The only estimate we have seen is that of Rutter (1903), who wrote that this elevation is "over 50 feet above the surface of the lake." It seems reasonably sure that the higher terraces represent a Pluvial lake, for they appear to be much older than the obviously Recent lower terraces. The latter may represent the high-water level of 1916, mentioned by Grinnell, Dixon and Linsdale (1930).

The fish evidence definitely calls for a surface-water connection between Eagle Lake and Lake Lahontan waters. It cannot be assumed that Eagle Lake was populated through the outlet tunnel that was operated for some time in an ill-fated irrigation venture, for the tunnel was not in operation until 1925 (Grinnell, Dixon and Linsdale, 1930), 8 years after Snyder (1917*a*) recorded from the lake all of the species, except *Richardsonius egregius,* which we have collected there. The trout, *"Salmo aquilarum,"* which Snyder described from Eagle Lake as an endemic representative of the Pacific-drainage rainbow trout series, appears from a re-examination of the types to have been based on hybrids between the native cutthroat and an introduced rainbow trout (*Salmo gairdnerii*). This conclusion is in line with expectation.

13.—Horse Lake.—This lake, also in Lassen County, California, was slightly larger as a Pluvial lake than it is now (Russell, 1885). In Pluvial and probably in Recent times it overflowed eastward and then southward into the Honey Lake arm of Lake Lahontan. In 1942 the level lay below the outlet even though a trench had been dug in the upper end of the channel in an effort to maintain a discharge for irrigation in the Honey Lake Basin. The two fishes of the Horse Lake basin, *Catostomus tahoensis* and *Rhinichthys osculus robustus,* are, as would be expected, typical Lahontan forms.

14.—High Rock Lake.—The intermittent lake known under this name lies in a stream channel that was obviously occupied by a Pluvial tributary of the Soldier Creek arm of Lake Lahontan. The damming of this stream by a landslide produced a lake considerably larger than the present bed (Russell, 1927*a*). According to Russell this lake drained itself by downcutting through the slide material. Russell also noted similar lakes, including the extinct Lake Jess (shown on map 1 west of Lake Surprise, no. 38, and north of Lake Madeline, no. 33), in the Pit River drainage.

The only fish in springs within the drainage basin of High Rock Lake is a *Rhinichthys osculus,* of a type that is rather noncommittal as to relationships.

Pluvial Lake Madeline (map 1, no. 33), which was claimed by Russell (1884, 1885) to have overflowed into the Honey Lake basin, seems to have had no Pluvial surface discharge (see p. 58).

15.—Lake Lemmon.—Silver Lake and other ephemeral lakes in Lemmon Valley, now a fishless basin, are obviously the remnants of a Pluvial lake about 8 miles in length by 3 miles in maximum width. Cross bars to the eastward and shore features, examined with Vincent P. Gianella on June 20, 1946, indicate that the lake discharged northeastward through Hungry Valley into a bay of Lake Lahontan. An abundance of metates and other artifacts indicates that the basin contained more water not very long ago. This Pluvial lake, which we name *Lake Lemmon,* has not been recognized previously.

Free (1914*a*) wrongly thought that the waters of Lemmon Valley discharged into Truckee River. He expressed the further opinion that Warm Springs Valley to the northeast may have been enclosed in Pluvial times, but that valley was occupied by the bay of Lake Lahontan into which Lake Lemion discharged. Furthermore the alluvial divide mentioned by Free is not conspicuous and maps show a continuous stream course from this valley through Mullers Pass into Pyramid Lake.

In Spanish Springs Valley just east of Lake Lemmon there is a playa and large area that is probably a lake bed. The pass to the southward is low and when viewed from the air the low part of the valley appears to have been tapped by an outlet channel, leading into Truckee River. The Spanish Springs basin seems to be fishless.

Drainage Relations of Lake Lahontan

Thorough field studies led Russell (1885) and almost all subsequent geologists to conclude that Lake Lahontan never had an outlet, but the ichthyological evidence definitely calls for a discharge into at least one of the major surrounding stream systems, or for some other type of surface-water connection across the Lahontan rim. In an effort to locate the physiographic evidence for a Pluvial overflow, we have followed Russell's journeys around the entire periphery of the Lahontan drainage basin, but nowhere have we found any definite indication of either the location or the time of the outlet.

That the discharge was southward into the Colorado system, as King (1878) and Whitney (1882) thought, and as Keyes (1918) recently hinted, is particularly improbable. The idea that such a connection existed is supported neither by the physiographic evidence nor by the fish data. The Lahontan and Colorado faunas have very little in common. The hypothesized outflow to the north, into the Alvord basin (Blake, 1872*a–b*), is deniable on the basis of the ichthyological as well as the physiographic data.

The physiographic and ichthyological evidence weighs heaviest toward the view that Lake Lahontan or its antecedent discharged northwestward, westward, or southwestward. There are rather strong resemblances between the Lahontan and Klamath faunas, but the respective drainages are separated in part by minor independent basins (pp. 58–67) and everywhere by Goose Lake and its outlet, Pit River, a Sacramento tributary. If Lake Lahontan did discharge through the Klamath the outlet was probably across the Modoc Plateau in northeastern California, which has since been covered by lava flows (Peacock, 1931; Anderson, 1941) and has recently become connected with the Sacramento system. The occurrence in the intervening Pit River of seeming relicts of Klamath relationships (p. 69) supports this view. On faunal grounds a direct connection with the Sacramento system seems less probable. The idea that the waters of Lake Lahontan were conjoined with those of the Death Valley complex seems perhaps as plausible as the theory of a connection between the Lahontan and the Klamath, on the basis of both zoogeographical evidence (p. 79) and of the paleontological evidence (p. 26, and Miller, 1945*c*). There is also a moderately strong agreement between the fish faunas of the Lahontan and the Bonneville basins, but there is no physiographic evidence for a connection, even along the short distance to the northward where the major drainage basins are not separated by minor ones (pp. 51–58). There are also faunal resemblances between the Lahontan and the Columbia, though the rather numerous highly distinctive Columbian species are not represented in the Lahontan basin. Several Recent fishes of the Lahontan system are interpreted as only subspecifically differentiated from those of each major adjacent basin.

The resemblances between the Lahontan fishes and those of the several surrounding open drainage basins are of such a nature as to indicate transfers of water and of upland fishes across already existing divides, by such processes as stream capture or stream migration. It has been suggested that by some such means a few Lahontan fishes appear to have made their way into certain Sierra Nevada tributaries of the Sacramento (Rutter, 1908; Snyder, 1917*a*). This transfer, if a natural one, was probably very recent, for the wanderers have not spread widely, nor have they become much if at all modified. Indeed both of us have unsuccessfully attempted to collect further specimens of the Lahontan species where Rutter and Snyder reported having found them. Transfer by man, with failure to become established, seems to be a more plausible explanation. We have learned of the recent introduction of Lahontan fishes, including *Siphateles o. obesus* and *Richardsonius egregius,* into the Sacramento system and Jordan (1922: 343) recorded the early transplanting of Lahontan cutthroat trout, *Salmo clarkii henshawi,* into the Sacramento system.

Several lines of evidence rather effectively negate the view that the faunal transfers back and forth took place solely over the surrounding rim of the Lahontan basin. In the first place we must consider the evidence that the Lake Lahontan fish fauna once included two now extirpated coastwise low-elevation types (*Fundulus* and *Gasterosteus*) that can not be assumed to have crossed a high divide (p. 26). In the second place we cannot overlook the circumstance that most of the 8 endemic species in the Lahontan fish fauna (discussed below) are lowland types, that are probably of considerable age and likewise cannot be thought capable of crossing an elevated divide. It seems highly probable that Lake Lahontan did have an outlet, either during a high Pluvial level that was so brief as to cut no lasting terraces, or, more probably, during the high level of an "earlier pluvial" precursor of the lake, so ancient that its shore features have been effaced by time.

We find no support for the suggestion by Keyes (1918) that the Columbia River has captured the main affluents of Lake Lahontan.

Summarizing many threads of physiographic, paleontological and ichthyological data, and anticipating a discussion of the Klamath fauna (pp. 67–69), we venture the following tentative inferences regarding the drainage relations between the Lahontan and the surrounding basins. In late Micocene and in Pliocene times the region of Lake Lahontan contained lakes and streams with essentially modern fish types. In the late Pliocene or early Pleistocene the whole area was so low that coastal fish types ranged from the southwest to Lake Lahontan. Great elevation then took place. Sometime during the Pleistocene, probably early, there was a connection on the "Interior Platform" between Lake Lahontan and the Klamath Lakes. Lavo flows occurred in the intervening region, and the connection between the two basins became broken. Subsequently, perhaps long afterward, the intervening Goose Lake basin lost the connection which it had maintained with the Klamath and became tributary to the Sacramento by the backcutting of Pit River. Either before or after that change in drainage, Klamath Lake rose high enough to overflow, bringing together interior and coastal fish faunas. At various times headwater transfers of water and fish life took place to and fro across the divides between the Lahontan and most if not all of the surrounding basins. Many of these ideas are supported by very tenuous evidence, but they are the most plausible that we can now propose.

Further Inferences from Consideration of Lahontan Fish Fauna

The high degree of endemism displayed by the Lahontan fishes—8 of the 13 known species are confined to the basin—indeed suggests a separation of at least much of the fauna since Pliocene or early Pleistocene time.

The most notably endemic Lahontan fish, representing a very distinct genus now being described (Hubbs and Miller, in press), is almost certainly confined to the warm springs of a single small basin that lies at the approximate level of the highest shore line of Lake Lahontan. We regard this odd little cyprinid as an ancient relict rather than as the product of sudden evolution. On this theory it has become extinct in most and probably all other parts of the Lahontan drainage system, and all near relatives have probably died out, in this and in other basins. Another interesting Lahontan endemic is a peculiar trout, *Salmo seleniris* Snyder (1933, 1934), which is native to a single small mountain stream, above a waterfall.

Several of the endemic Lahontan fishes, including a remarkable sucker (*Chasmistes cujus*), two silvery trouts (*Salmo regalis* Snyder, 1912, and *S. smaragdus* Snyder, 1917a) and one minnow (*Siphateles obesus pectinifer*), are modified for life in lakes, and were probably evolved either in Pluvial lakes Lahontan and Tahoe or in prior lakes in the same region. The *Chasmistes* and *Salmo smaragdus* are now confined to Pyramid Lake, except that in the spring the sucker migrates up Truckee River. The fact that they occur in Pyramid Lake was taken by Snyder (1914, 1917*a*), Antevs (1925), Jones (1925) and Hutchinson (1937) as evidence contradictory to the theory of Russell (1885) and Huntington (1925) that Pyramid Lake owes its freshness to post-Lahontan desiccation. Hutchinson disagreed with Huntington's view that the Pyramid lake fishes could have persisted in the lake-like mouth of Truckee River, over a period when the lake water became highly concentrated, and we are inclined to favor Hutchinson's argument.

The lacustrine minnow, with numerous gill-rakers, was treated by Snyder (1917*a*) as the type of an endemic genus, *Leucidius*, but we regard it as only a subspecies of *Siphateles obesus* (Hubbs and Miller, 1943). The reasons for this altered interpretation are the discovery that this lake-type chub is connected with typical *obesus* by a chain of intermediate forms and the inference that the two interbreed freely. Since the waters have dwindled, and the lake and creek types have been forced into cohabitation, the two have hybridized very extensively. We have referred to this specific breakdown in connection with our analysis of a similar case of hybridization in the Mohave Desert (Hubbs and Miller, 1943). The two cases still seem somewhat comparable, even though we now believe that the cohabitation and hybridization of the Mohave River minnows dates only from the introduction by man of *Gila orcuttii* into a stream formerly inhabited only by *Siphateles mohavensis*.

Glimpses of the Postpluvial history of the Lahontan fishes have recently been seen in a preliminary examination of dried fish remains from Humboldt Cave, kindly made available to us by Dr. E. W. Gifford of the University of California. This dry cave, with evidence of an Indian culture similar to that elaborately described for Lovelock Cave by Loud and Harrington (1929), yielded many fish remains in a remarkably fine state of preservation. These, we may assume, represent the ancient fish fauna of the region, presumably that of Humboldt Lake or the lower Humboldt River. The antiquity is to be dated by centuries and perhaps by millenia. The remains include the posterior part of a large sucker, presumably the lacustrine *Chasmistes cujus* (now confined to Pyramid Lake) and many chubs (*Siphateles*). The chubs include hybrids (intergrades) between the lacustrine *S. obesus pectinifer* and the fluviatile *S. o. obesus,* whereas at the present time only *S. o. obesus* occurs in this part of the Humboldt River system. We are thus led to conclude that at the ancient time of the occupancy of Humboldt Cave, Humboldt Lake was a relatively large and perennially fresh lake. Rather sharp annuli on the scales indicate that there were marked seasonal differences in temperature. The long period of time during which the two types of *Siphateles* have been hybridizing is of special interest to students of speciation, because it shows that such hybridization, although producing what we have good reason to regard as fertile offspring, may continue almost indefinitely without leading to a fusion of the two interbreeding types. Through the further study of such fish remains from Indian deposits, along with research on the living and fossil fishes, we may eventually be able to reconstruct in considerable detail the changing fish faunas of the alternately watery and arid Lahontan basin and to make plausible inferences in regard to the past hydrography and the past climate of the region.

PLUVIAL LAKES IN ENCLOSED BASINS SURROUNDED BY LAHONTAN WATERSHED

Five Pluvial lakes appear to have existed in enclosed basins that were entirely surrounded by the drainage basin of Lake Lahontan. The basins of these lakes are now devoid of native fish life.

16.—Lake Wellington

Another Pluvial lake probably occupied the now apparently fishless[5] basin of a dry alkali flat, 11 to 13 miles north of Wellington. Its form and position are perhaps best shown on the U. S. G. S. Reno and Sierraville Quadrangles (where the basin is called Warm Spring Valley). The dunes and low terraces of *Pluvial Lake Wellington,* as we may call this small body of water, all seem to lie below the level of the low alluvial divide leading south toward the West Fork of Walker River.

17A.—Lake Laughton

Near the California line 14 miles northwest of Reno, Nevada, is the remnant of what may be called *Pluvial Lake Laughton.* The basin is rather well shown, as Laughton Valley, on a map (2″ and 3″) in Topographical and Land Classification Atlas Sheets, U. S. Geographical Surveys West of 100th Meridian (Wheeler Survey) 1878 (Atlas Sheet 47D). This lake formed terraces that were estimated by cursory field examination to be about 30 feet higher than the present lake bed. These shore features encircle the entire lake bed, and form a broad plain at the north end of the basin, at the mouth of the main tributary canyon. The only springs in the basin are hillside seeps on the south side that are piped to a ranch house, and Cold Spring, which proved to be fishless. The basin was probably an enclosed one in Pluvial as well as in Recent time, though it may have ephemerally risen to discharge over a low saddle into Long Creek, which is tributary to Honey Lake (see Reno and Sierraville Quadrangles, U. S. G. S.).

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[5] By "fishless" we mean devoid of native fish life. Few permanent waters have been neglected in the introduction of exotic species, which have no bearing on present considerations.

17B.—**Lake Fred**

Just north of the Lake Lemmon basin (p. 38) and on the east base of Fred Mountain, is a well enclosed basin nearly 6 miles long that contains playas. Dunes, bars and other lake features indicate that these playas are remnants of a Pluvial lake about half as long as its basin. This we call *Lake Fred.* The 6 passes, to different parts of the Lahontan system, are each at least 200 feet too high to represent a Pluvial outlet. The lowest pass is probably to the southeast, into Hungry Valley.

18A–B.—**Lake Kumiva and Granite Springs Lake**

Two separate Quaternary lakes were mapped by Russell (1885) on the main island in Lake Lahontan, respectively in Kumiva and in Granite Springs (or Blue Wing) valleys. King (1878) had mapped these waters as parts of Lake Lahontan and Russell (1883) had earlier indicated them as playas. Without citing evidence, Free (1914*a*) stated that the divides between these basins and the Black Rock division of Lake Lahontan were overtopped by the highest levels of that inland sea. He was in error by several hundred feet. The depth of the Granite Springs depression is shown on the Lovelock Quadrangle (U. S. G. S.). The divide north of Kumiva Lake, near twin lava buttes, was found to be much higher than the highest Lahontan terrace and definitely higher than the terraces of the lake in Kumiva Valley ("White Sand" basin according to Flint, 1947) and there is no outlet channel. We call the more northerly of the two waters *Pluvial Lake Kumiva* (from the name, also spelled Kumavi, of the valley and the adacent peak) and the more southerly one (18B), *Pluvial Granite Springs Lake* (from the name of the basin). Lake Kumiva (18A) produced terraces and dunes that remain to indicate that it was larger than has previously been thought. The position and size as shown on the map are rough approximations. When examined on June 21, 1946, both basins appeared to be wholly fishless.

MINOR LAKES JUST SOUTH OF LAKE LAHONTAN SYSTEM

Just south of the tortuous divide which confined the Lake Lahontan drainage system at its maximum extent there lie a number of smaller enclosed lake basins which may have had an "earlier pluvial" or a very temporary Pluvial connection with Lahontan waters. Some such connection is indicated by the composition of the fish faunas of the three basins of this category that contain native fish.

19.—**Fish Lake**

This western Nevada basin, containing the bed of what may be called *Pluvial Fish Lake* (map 1, no. 19), is separated by only a low saddle from Columbus Salt Marsh, which in turn is set off by a moderate divide from the trough containing Rhodes Salt Marsh, Soda Spring Valley and the Walker Lake arm of Lake Lahontan. The whole form a series, from south to north. Fish may have entered Fish Lake from Lake Columbus by way of Gap Springs on the summit of the intervening saddle. Free (1914*a*) assumed a discharge over this gap, but the highest terrace seems to be lower than the summit. Lake Columbus may well have contained fish; they are known to have lived there during an earlier (Esmeralda) time (p. 46).

Two forms of *Siphateles* were found in Fish Lake Valley. One, a lacustrine type, seems to be an endemic subspecies, perhaps now extinct. The other, a stream type, is so much like the Owens River form that we suspect it was introduced as a bait minnow. The remnants of Fish Lake have now been stocked with exotic fishes, including largemouth bass and carp. That some minnow was native is almost proved by the fact that the marsh and springs were early named "Fish Lake."

20–21.—**Lake Dixie and Lake Labou**

Formerly known also as Osobb Valley and as Salt or Salt Springs Valley, Dixie Valley in central Nevada contains the sump (Humboldt Salt Marsh) of a relatively large desert drainage, which is bounded on all sides except the south by the Lahontan drainage basin. To the southward lies what we call the Area of Sterile Basins. Even in Pluvial times the Dixie basin was probably a rather arid region. As Gale (1913*a*) wrote, this basin apparently did not contain a deep lake. Gravel bars and terraces, however, indicate that Humboldt Salt Marsh was covered by a shallow lake, for which we propose the name, *Pluvial Lake Dixie* (map 1, no. 20). Free (1914*a*) stated that there are strand lines 150 and 40 feet above the playa level, but others have not recorded evidences of a deep lake and we saw none. The only native fish life found in this great arid expanse is a probably endemic subspecies of *Siphateles obesus,* which occupies, so far as we could determine, a single small spring—one of several in the tributary Pleasant Valley (Hubbs, 1941*a*). Presumably this fish is related to a Lahontan subspecies of *S. obesus.* The carp which inhabit a spring in Dixie Valley are so peculiar in appearance and so dwarfed as to lead us to wonder if they may not represent the product of speciation within historic time.

One fishless basin, just to the southward, is generally mapped as Fairview Valley. It contains Labou or Frenchman's Flat, the remnant of a Pluvial lake (map 1, no. 21). This lake was mapped by Russell (1885) and by Meinzer (1922). As Free (1914*a*) suggested, it may well have had a connection with Lake Dixie, across the low intervening saddle. For this small body of water we propose the name *Pluvial Lake Labou,* after the present "flat," which in turn was named for a French settler.

22.—**Lake Toiyabe**

The basin of Big Smoky Valley that lies between the Toiyabe and the Toquima ranges in central Nevada was the site of a deep Pluvial Lake (Russell, 1885). This water was carefully mapped by Meinzer (1916, 1917), who named it Lake Toyabe. We use the spelling Toiyabe, to conform with a decision of the National Board on Geographic Names.

The remnants of this Pluvial lake are inhabited by two species of native fish (cutthroat trout have been introduced—see Miller and Alcorn, 1946: 175–176). One of these, a *Rhinichthys,* we have as yet been unable to distinguish from the Lahontan form. The other, *Siphateles obesus,* is represented by two endemic subspecies. One type occurs in the springs along the west side of the old lake bed, the other in Charnock Springs on the east side. The two kinds are separated by only 4 to 8 miles of level sand-coated playa. Fishes of this type would surely have constituted a uniform population, occupying the entire lake area, whenever it became covered with moderately fresh water. It is plausible to assume that such a connection between the western and eastern springs took place within a few hundred, at most a few thousand years (but not, however, within the memory of the oldest settlers). Complete isolation and the intense inbreeding of very small populations has obviously resulted in very rapid speciation (p. 24).

Both the *Rhinichthys* and the *Siphateles* may have reached Big Smoky Valley from the Lahontan system. There is a moderately low pass from Big Smoky Valley northward into Grass Valley, in the basin of Pluvial Lake Gilbert (map 1, no. 5), which, we think, discharged into the Lahontan basin (p. 5). What appears to be a stranded stream terrace extending northeastward across this divide may well represent the Pluvial discharge of a stream into Grass Valley. The present channel swings abruptly to the southward to lead, via Rye Patch Canyon, into Big Smoky Valley (see Roberts Mountain Quadrangle). By the previous stream course Lahontan fishes may have reached Big Smoky Valley. Contradictory to this view, however, is the strong differentiation of the *Rhinichthys* in Grass Valley and the fact that the outlet of Pluvial Lake Gilbert was so steep as to make it seem unlikely that *Siphateles* could have made its way into that lake. To the southward Big Smoky Valley is separated by only a very low valley saddle from Peavine Creek, in the drainage of Pluvial Lake Tonopah (see p. 48), in the "Area of Sterile Basins."

23.—AREA OF STERILE BASINS

Other small enclosed basins, all now devoid of native fish life, occupy a band across Nevada south of the Lahontan and other systems that do support fishes. In clockwise order the fish-inhabited drainage systems that surround this "Area of Sterile Basins" (designated by number 23 on map 1) are: the enclosed basin of Pluvial Lake Dixie (no. 20 on the same map); the headwaters of Reese River, a Lahontan tributary; the separate drainage of Lake Toiyabe (no. 22); the main tributary of Lake Diamond (4), of the Lahontan system; the independent drainage of Railroad Lake (60); the Pluvial White River system (61); the Las Vegas River system (67); the Death Valley system (43 to 56); the small basin of Fish Lake (19); and the Walker Lake arm of Lake Lahontan (2). We might have included several other contiguous fishless Pluvial lake basins that are discussed under the headings of adjacent fish-containing valleys. These are the basins of Lake Labou (21), which may have discharged into Lake Dixie (p. 44); Coal Lake (62), which, like 2 or 3 lake basins just east of Pluvial White River, may have briefly drained into that stream (p. 96); East Lake (68C), one or two other lakes (68A–B) in the same valley and Indian Springs Lake (69), which are considered in connection with Pluvial Las Vegas River (p. 100); and lakes Mono (43), Aurora (44) and Adobe (46), which are treated under the heading of the Death Valley system (pp. 77–88).

There are three other major areas of fishless basins in the arid southern part of the Great Basin. These now almost waterless depressions (pp. 88–90) adjoin the Death Valley system. One lies west of the Mohave River system, between that drainage and the coastal streams of southern California. Another group lies between the Death Valley system and Fish Lake Valley. The third intervenes between the Death Valley system and the Colorado River. Various isolated basins east and south of the Colorado River, including that of Red Lake (70), are also devoid of fish life.

Although we have not examined several basins in the southern part of the Area of Sterile Basins, we have obtained an abundance of convincing local testimony and many suggestions from articles and maps, all of which indicate that the entire area is totally devoid of fish life. Much of this forbiddingly arid region (Chapman, 1906) was probably as fishless during Pluvial times as it is now. Even when the beds of Lake Bonneville, Lake Lahontan and several other lake bottoms not far to the northward were deeply covered by water, all but the northwesternmost part of the Area of Sterile Basins was too arid for the development of deep and perennial lakes (Meinzer, 1922). Most of the rather numerous dry lakes in the region were probably covered by water much of the time (Russell, 1896), but these lakes were probably too shallow or too ephemeral to have supported fish life or to have overflowed the enclosed basins. Several of the more northwestern basins in the fishless area were flooded by Pluvial lakes (see maps and discussions by Russell, 1885; Bailey, 1902; Spurr, 1903; Ball, 1907; Gale, 1913*a–b*; Free, 1914*a*; Carpenter, 1915; Meinzer, 1917, 1922), but fishes either did not reach these basins or have not persisted there. Reasons why some of the basins are fishless are given in the discussion below.

The entire Area of Sterile Basins has not always been fishless. Some of the more southerly basins may have been connected with the fish-inhabited waters of White River and Las Vegas River, as Free (1914*a*) indicated without adequate supporting evidence. Lake Columbus presumably had fish, for it probably was connected just to the southward with Fish Lake (map 1, no. 19), which contains an apparently indigenous chub (p. 44). In Pliocene time the region about Columbus Lake was supplied with fish life, for fossil fish are known from the Esmeralda Formation in this basin. Among the specimens that we have examined from this Formation we recognize what seems to be a catostomid fish as well as a seemingly lacustrine minnow. This cyprinid was named *Leuciscus turneri* by Lucas (1900) and was discussed further by Eastman (1917). The age of the fish-bearing deposit was discussed by Stirton (1932).

A–G.—Basins Adjacent to Lake Lahontan

Two fishless basins lie between the Lake Dixie and Reese River drainages and five are located along the eastern edge of the Walker Lake division of the Lahontan system. All lie among mountains and each is supposed to have contained a Pluvial lake (one had 3 or 4 more or less disconnected lakes). There are no good indications that during Pluvial times any of these basins in Nevada had any surface-water connection with any other waters.

Of these seven basins, the northernmost, located in eastern Churchill County southeast of Lake Dixie (map 1, no. 20), was occupied by a Pluvial lake mapped as about 18 miles long (Russell, 1885; Free, 1914*a*; Meinzer, 1922). This Pluvial water body (map 1, no. 23A) may be called *Lake Edwards,* after the Edwards Creek basin in which its indications occur. The drainage area was examined and found fishless. There is no verification for Free's (1914*a*) view that Lake Smith discharged into Lake Edwards.

Just southeastward from Lake Edwards, in Smith Valley, Lander County, there appears to have existed another Pluvial lake (same references), which may be called *Lake Smith* (map 1, no. 23B). It was treated by the same authors. This lake was probably about 10 miles long. Its basin was also traversed and found to be devoid of native fish life. The trout in Smith Creek were definitely reported to have been introduced. There are no indications of any former connections between either basin and the tributaries of Lake Dixie to the west, of Reese River to the east, or of lakes Tonopah and Gabb to the south. A Prepluvial discharge into Ione Valley of the Tonopah drainage is suggested by physiographic evidence (Free, 1914*a*).

Gabbs Valley was the site of a Pluvial body of water about 10 miles broad that may be known as *Lake Gabb* (map 1, no. 23C). It was mapped by Russell (1885) and Meinzer (1922), and we have modified the outline in accordance with the Hawthorne Quadrangle (U. S. G. S.) and from personal observations. The depression is devoid of fish life for very obvious reasons. The rim of the Gabbs basin is too high and sharp to have been crossed anywhere by fish, and any that might have gained entrance could no longer persist, for the only surface water of consequence here is a spring much too hot to support fish life. Gabbs Valley is in Mineral County and is the first basin east of the Walker Lake arm of Lake Lahontan.

South of Lake Gabb, in the trough that connects the Walker Lake arm of Lake Lahontan with the Lake Columbus basin, Russell (1885) and Meinzer (1922) indicated a narrow Pluvial lake (map 1, no. 23D′+D″) about 20 miles long. On his map of Pleistocene lakes, Jones (1940) labelled this body of water "Spring Lake," but he used the same name for another lake (p. 56). Our examinations of the basin lead us to believe that the 4 present playas represent 3 Pluvial lakes. The northernmost and westernmost of these lakes, which we may name *Lake Acme* (map 1, no. 23D), from the name of the railroad station, is represented by a playa, with some dunes on the north side. Its shoreline was probably at about the 4,400 foot contour (Hawthorne Quadrangle, U. S. G. S.) and there are no indications that it rose high enough to overflow westward, as Free (1914*a*) thought, into the Walker Lake arm of Lake Lahontan or eastward into Lake Luning. Had it done so, outlet-level terraces should have been produced. The playas about Luning and Mina appear to have been united into a single lake, because they are connected across the low intervening area by a series of dunes. This body of water we call *Pluvial Lake Luning* (23D′). We found no evidence to confirm Russell's view that this lake was a part of a large lake also overflowing the Rhodes Salt Marsh, which is about 100 feet lower. A definite outlet channel just east of Sodaville shows that Lake Luning long drained into *Lake Rhodes,* as we call the sump basin (23D″). A 6-foot excavation on the basin of Lake Rhodes, about 47 feet above the playa floor and below the level of the inlet channel, shows only alluvial-cone material. There is no evidence that Lake Rhodes discharged during the Pluvial period. A depth of more than 200 feet would have been required to effect an outflow into Lake Lahontan. The few small springs in this compound basin are all fishless.

Three other lakes lay adjacent to the Lahontan watershed, each in a small well-enclosed basin in the mountains of Mineral County, Nevada. The northernmost, which may be called *Lake Garfield* (map 1, no. 23E), lay west of Lake Rhodes on Garfield Flat (formerly Excelsior or Excellsior Flat). It was mapped but not named by Russell (1885), Meinzer (1922) and other geologists. Another lake was located at the site of Teels Marsh west of Lake Columbus. It may be named *Lake Teel* (map 1, no. 23F). A third Pluvial lake (map 1, no. 23G) existed in Huntoon Valley, a mountain basin between Lake Teel and Lake Mono (map 1, no. 43). It was shown as a Quaternary lake by Russell (1885) and his followers, and may be named *Lake Huntoon,* for the valley in which it occurred. These lakes were either too shallow, or more likely too inconstant in level, to produce lasting beach features, other than small dunes. Dunes are particularly well developed around the south and east sides of Lake Teel, which is now represented by stretches of marsh, whereas the two other playas are usually dry. Rounded cobbles on the greasewood slopes above the playa of Lake Garfield suggest that the Pluvial lake was larger than the present dry lake. There seems to be no clear proof that any of these enclosed lakes was permanent during the Pluvial period. None contain fish.

H–K.—**Basins Structurally Connected with Basins of Lake Toiyabe and Fish Lake**

To the east of the lakes just discussed there lay a chain of 4 lakes in basins with low intervening divides. The compound basin was barely separated from 2 of the minor, fish-inhabited waters—Lake Toiyabe (map 1, no. 22) to the north and Fish Lake (no. 19) to the south. There are no proofs, however, that fish passed over any of the low divides in Pluvial times.

In this group we include Monte Cristo basin (map 1, no. 23H), which adjoins the basins of Lake Gabb and Lake Rhodes and is related more closely to the drainage of Lake Tonopah. At the lowest point the separating divide is less than 400 feet high (Free, 1914*a*). In view of its mountainous surroundings and of its location between other basins that did contain Pluvial lakes, it is thought that the present dry bed represents a lake, which we may name *Pluvial Lake Monte Cristo,* that was at least semipermanent. There is no reason to suppose, however, that the basin overflowed in Pluvial times. It was probably fishless then, as it now is.

As already mentioned (pp. 43 and 46), Lake Columbus (map 1, no. 23I) may have been connected in Pluvial times with Fish Lake just to the southward. It may, therefore, have contained fish life in Pluvial times, as the basin certainly did in the Pliocene. If so, the fish have been unable to persist in the limited waters of Columbus Salt Marsh, which is the remnant of the Pluvial lake. This lake has been mapped since the time of Russell (1885), and it as well as the present marsh was treated in detail by Hicks (1915), who proposed the name, Lake Columbus.

The Lake Columbus basin is separated by a low divide from that of Lake Tonopah (Meinzer, 1916, 1917), but there is no evidence to support the suggestion of Dole (1913) that the Pluvial waters rose high enough to produce a strait between these lakes or to indicate that Lake Columbus discharged into Lake Tonopah (map 1, no. 23J). Such a connection, however, may have existed at some "earlier pluvial" time. Lake Tonopah may have received fish from Lake Toiyabe, for these lakes were separated only by a low alluvial divide, across which stream and fish transfers may have occurred. Sizeable creeks from the mountains to the east must have crossed the alluvial saddle, but if fish were thus introduced into the basin of Lake Tonopah, they have apparently been unable to persist in any of the tributary waters. We did not, however, thoroughly explore the live springs about Cloverdale.

If fish were present in Lake Tonopah waters they may also have invaded Clayton Valley, since again there is only a low intervening divide across which creeks may have wandered. No fish other than introduced carp, however, were found in Silver Springs Marsh, which contains the only permanent surface water in Clayton Valley. Meinzer (1917) doubted that a Pluvial lake formed here, but the extensive salty playa east of the marsh suggests that a Pluvial lake that was at least semipermanent occupied the floor of the valley. This body of water may be known as *Pluvial Lake Clayton* (map 1, no. 23K). This was the lowest water in the series of basins just treated, but Meinzer found no evidence to support the idea of Dole (1913) that Lake Tonopah drained into Lake Clayton.

L–T.—**Basins Structurally Connected with Death Valley System**

Proceeding eastward the next group of structurally interconnecting basins ties in most closely with the Death Valley system. The central series of basins, comprising Ralston Valley, Stonewall Flat and Sarcobatus Flat (map 1, no.

, L—P—P′—R), has much the appearance of an old river channel fragented by alluvial flows or crustal movements. King (1878) and some other rly geological explorers mistook this chain of valleys for an outlet of Lake hontan. Russell (1885) made it clear that the Pluvial lake did not discharge this direction. Although he did not regard these valleys as being the outlet annel of Lake Lahontan, Free (1914*a*) included them in the Amargosa stem (p. 84) of the Death Valley complex and implausibly suggested that e connection was "post-Lahontan." Keyes (1918) suggested that the depth the Amargosa Canyon indicated that Lake Lahontan may have drained rough the Amargosa River. There are no indications, however, that Sarbatus Flat filled deeply enough to overflow during Pluvial times across the tervening divide into the Amargosa. Toward the east this basin, as well as ld Flat and Kawich Valley, is separated by well-defined divides on the high ahute Mesa from the head of Amargosa River and its tributary canyons ee U. S. G. S. Quadrangles and map in Ransome, 1907). On the west side, wever, there is a rather low gap in the Sacrobatus rim. It leads into the eep Grapevine Canyon, tributary to the main northern tributary of Death alley. The possibility of an "earlier pluvial" discharge through this canyon, om the Ralston–Sacrobatus Flat basins and possibly even from Lake Lahonn should be investigated, even though a Pluvial overflow seems implausible. this connection it should be remembered that both Recent and fossil fishes dicate that there have been surface-water connections between Lake Lahonn (or an antecedent sea) and the Death Valley system.

What connections may have existed between the basins of this group is t wholly clear. The main headwaters lie in Ralston Valley (map 1, no. 23L), ich is tributary to Mud Dry Lake. This was perhaps a semipermanent Plual lake. The dry lakes in Cactus Flat (23M) and the sumps of Salisbury ash (Schrader, 1913) may also have constituted a shallow Pluvial lake, ich may have discharged westward into the sump lake of Ralston Valley. kali Spring Valley (23O) to the westward (the "Goldfield Basin" of Free, 14*a*) is definitely enclosed, but also opens into lower Ralston Valley. Gold at (23N), which, like the other basins, may have had a shallow Pluvial lake, ens northward into Cactus Flat. There is only a low divide between Raln Valley and Stonewall Flat, which has 2 main sumps (23P and 23P′) at may or may not have had separate drainages in Pluvial times. A small alley (23Q) to the westward opens into the lower Stonewall Flat basin, which n turn is not very sharply separated from Sacrobatus Flat (23R). These asins have been traversed sufficiently to make us feel rather confident that hey are all fishless.

Two fishless basins, each with a dry lake, are structurally connected with he Amargosa system. These are Yucca Flat (map 1, no. 23S) and Frenchman Flat (no. 23T). Free (1914*a*) held that the Yucca Basin is separated rom Frenchman Flat to the south only by an alluvial divide less than 100 eet higher than Yucca Dry Lake. He believed that there once was a drainage across this divide, but it seems very improbable that there was such a discharge in Pluvial times. Frenchman Flat in turn is separated from the Amargosa River system by a divide so high that even Free did not assume a discharge. The structural relations just mentioned are confirmed by a map prepared in 1945 by the Indian Springs Army Air Field.

U–V.—Basins Adjacent to Railroad Lake System

A series of sterile basins surround the south half of the large drainage basin of Pluvial Railroad Lake (map 1, no. 60). These basins are poorly known physiographically and have been incompletely explored—some never even visited—by biologists. Local testimony, however, has yielded no hope that any of the basins will be found to contain fish life.

In counterclockwise sequence these divisions of the Area of Sterile Basins (map 1, no. 23) are as follows:

23U.—The basin of Willow Creek has a dry lake that was possibly more or less permanent in Pluvial times. In all probability this was then an independent drainage basin.

[23M–N.—Cactus Flat and Gold Flat are considered above, as elements of the basins structurally connected with Death Valley.]

23V.—Kawich Valley is structurally continuous with Railroad Valley, though it is separated by a divide that is far too high (see Kawich Quadrangle, U. S. G. S.) to verify Free's claim (1914*a*) that it was included in the Pluvial drainage of Railroad Lake (see p. 94).

[23W.—Penoyer or Sand Spring Valley is treated below, because of its indirect structural connection with Pluvial White River.]

[62.—The basin of Coal Lake opens toward White River and in Pluvial times was possible tributary to that stream. It is discussed on p. 98.]

W–Z.—Basins Structurally Connected with Pluvial White River

In the southeastern tongue of the Area of Sterile Basins there are 6 other arid basins which are connected with one another and eventually with the valley of Pluvial White River (p. 96) by low divides. These structural relations have not been well known, or not even suspected, but are shown on a map of southern Nevada prepared in 1945 at the Indian Springs Army Air Field, Las Vegas. Each of the 6 basins has a dry lake, but all are now excessively arid and no Pluvial interconnections seem probable, except perhaps from Papoose Lake (23X) into Groom Lake (23X′) of Emigrant Valley (formerly Tim-pahute Valley). The lowest pass out of that valley is into Desert Valley (23Y), from which a low pass leads into Pahranagat Valley in the course of Pluvial White River. Free (1914*a*) included Emigrant and Desert valleys together, but he used the name "Desert Valley" for Bristol and Delamar valleys (map 1, 63 and 64; also called "Dry Lake Valley"), on the opposite side of White River. Old maps used the same name, "Desert Valley," for a narrow trough shown still farther east.

The northernmost basin of this series, Penoyer or Sand Spring Valley (map 1, no. 23W) is separated from Railroad Valley (no. 60) to the northward and from Desert Valley (no. 23Y) to the southward by low divides, indicated by arrows on map 1.

As is suggested on p. 92, there are ichthyological reasons for believing that Penoyer Valley is part of a very ancient ("earlier pluvial") drainage course from Railroad Valley into White River. Unhappily, it is reasonably certain that it is now fishless.

Two minor basins (map 1, nos. 23Z and Z′), each with a dry lake, lie at the southeastern tip of the Area of Sterile Basins. They appear to be slightly disconnected from the Desert Valley system and if so, are surrounded by Colorado River tributaries. The northern basin (Z) may discharge at times into Dry Lake (Z′), of the southern basin, for suggestions of a dry-channel connection were seen from the air in 1947. This possible connection lies ound the western side of a hill between the two basins, but it is possible at the connection, if one existed, lay near the position indicated on map 1. or is it certain that the more northerly lake (Z) did not discharge northard into Pluvial White River. No evidence was found to indicate that the mall body of water which probably occupied Dry Lake Basin ever reached level high enough in Pluvial times to overtop the definite alluvial divide etween it and the California Wash drainage, which leads to the lower part Pluvial White River. Free (1914*a*), however, treated it as a very recent- disrupted part of the Muddy (Moapa) River system. He called the valley Gannett" Basin ("Gannet" on his map), apparently because he misread the ame, Garnet, of a local railroad siding.

With one or two possible exceptions each of these valleys contains a dry ke, but no indications have been found to suggest that any of the playas ere deeply and permanently covered with Pluvial waters. We have traversed nly the southernmost of the basins, but the testimony of local residents has een unanimous in indicating that all these basins are totally devoid of fish fe. This evidence is confirmed by Dr. Richard M. Bond, of the Soil Conseration Service, who has travelled extensively in the Area of Sterile Basins, xamining springs.

It is by no means assured that all of these southeastern sterile basins were arts of the Great Basin throughout Pluvial times. Some may have discharged nto either the White or the Las Vegas River. A direct connection with the olorado was precluded, for the California Wash tributary of Pluvial White iver had a common divide with tributaries of Las Vegas River. On the other and, Coal Lake (map 1, no. 62) and Indian Springs Lake (no. 69), considered ere as subsidiary respectively to White River and to Las Vegas River, may ot have discharged. If they did not overflow their basins, these lakes should added to the group (23) here under treatment.

LAKES BETWEEN LAHONTAN, BONNEVILLE AND COLORADO SYSTEMS

As noted by Russell (1885) the two largest units of the Great Basin ainage complex adjoin only to the northward, along a short common divide ear the Utah–Nevada line. Here there is an abrupt faunal break. Elsewhere e Lahontan and Bonneville drainage systems are completely separated by series of lake-containing mountain-rimmed basins (map 1, nos. 24–32), which ow little physiographic evidence of Pluvial overflow connections with one nother or with the watersheds of any of the three surrounding major ystems. So far as known the waters of these smaller basins have not been onnected in any way with the Lahontan tributaries, which flow to the westward on the opposite side of a mountain chain (comprising the Humboldt, Ruby and White Pine mountains). There is no valid basis for Free's (1914*a*) view that this long mountain barrier forms the western boundary of the Bonneville basin. Throughout the Pluvial periods these small basins seem to have remained separate from the Bonneville waters across the Toana–Goshute–Snake range to the east (see map 1). Nor was there any abvious linkage with the Pluvial tributaries of the Colorado (pp. 94–102) that lie to the southward.

The ichthyological evidence on the former hydrographic connections of the basins in this group is more definite than are the physiographic indications. In the valleys that comprise the four larger Pluvial drainage systems (see map 1), there occurs in common a type of dace that is so distinctive as probably to warrant generic separation from *Rhinichthys*. This evidence suggests that these basins have been interconnected in some way but that as a group they have long been isolated. Possibly they are the remnants of an ancient Prepluvial drainage system, of which Steptoe Valley may represent the main channel. More plausibly the peculiar fish type was first isolated in Ruby Valley and was then transferred by stream connections to the other valleys. In the following discussions some evidence is presented for such a transfer from Ruby Valley (map 1, no. 24) to the basin of Lake Waring (no. 28). There was probably a temporary Pluvial or an "earlier pluvial" overflow into Clover Lake (no. 26). Or the movement may have been from Steptoe Valley (Lake Waring) to Ruby Valley and thence to Clover Valley. How this fish type got into Spring Lake (no. 30) is at present inexplicable.

This distinct type of dace is rather degenerate. If it is really related to *Rhinichthys,* it has lost adaptations for riffle life that are generally characteristic of that genus. It is adapted, in contrast, for life in the small isolated springs that now feature the arid region in which they dwell. Great Basin minnows have undergone such modification along several independent lines, all leading to end results that are much alike (Hubbs, 1940*a*: 201; 1941*b*: 187).

There are doubts as to the hydrographic relations of the three fishless basins that are treated in this group. The basin of Antelope Lake (p. 55) may have been connected more closely with Lake Bonneville than with Lake Waring. That of Lake Jake (p. 57) might better be treated among the disjunct units of the Pluvial White River system. Long Valley (p. 57 was probably connected more closely with Lake Franklin than with Lake Jake.

24–25.—**Lake Franklin and Lake Gale**

A large area on the east side of the lofty Ruby Mountains constitutes the drainage basin of Pluvial Lake Franklin (map 1, no. 24), which was named by Sharp (1938). This ancient sea is now represented by two ephemeral lakes, Ruby and Franklin. The only native fish of this area comprise local populations of the peculiar genus mentioned above. They occur in the marshes of the Recent Ruby Lake and in springs throughout Butte Valley.

Some geologists (Clark and Riddell, 1920; Meinzer, 1922) have indicated that Butte Valley is the site of a Pluvial lake without an outlet, but the "lake" they crudely mapped, in the lower or northern part of this valley, was correctly shown on the maps of Russell (1885) and Gilbert (1890) as a bay of Pluvial Lake Franklin. We have followed the contours and have roughly charted the shore line of this large embayment (map 1). The southern part of the valley was tributary to the bay.

Altimeter readings indicate that at its maximum height Lake Franklin rose to within about 20 feet of the lowest summit, in Wells Fargo Canyon, between Pluvial Butte Bay and Clover Valley. We suspect that there was once an overflow in that direction (northward), but at so remote a period, or for so short a time, as to leave no clear physiographic evidence of an outlet channel or of beach lines at the outlet level. According to our altimeter estimates this pass is about 230 feet lower than Goshute Pass, over which Free (1914*a*) blithely ran the "Lahontan period" discharge of Ruby Valley into Steptoe Valley and thence into Lake Bonneville. He even favored a stream passage rather than a lake discharge over Goshute Pass, because (for some unaccountable reason) he failed to see any signs of a Pluvial lake in Ruby Valley. Free correctly guessed, however, that Butte Valley was formerly tributary to the Ruby basin.

Although the Butte Valley "lake" of Clark and Riddell proves to have been merely a part of Lake Franklin, we discovered that a Pluvial lake (map no. 25) did exist in this valley. It lay near the middle of Butte Valley, south of Pluvial Butte Bay. Its bed is crossed by the boundary line between Elko and White Pine counties, Nevada. The outlines of the lake were sketched from field observations and are especially unreliable for the southeastern shore. This body of water existed long enough to leave shore features, and then drained itself almost completely by the downcutting of its outlet through the alluvial dam. Particularly strong terraces occur in the region of this outlet cut. Springs in the lake bed yielded the type of dace discussed above. We suggest that this rather large impoundment be known as *Pluvial Lake Gale,* in recognition of Hoyt S. Gale's significant contributions to Great Basin hydrography. The names Butte Lake and Butte Valley Lake were used by Bailey (1902) for an "ancient lake" in California.

26.—**Clover Lake**

A Quaternary lake in Clover Valley, Nevada, lying just northeast of Lake Franklin, has been mapped since the time of Russell (1885). The waters of *Pluvial Clover Lake* (map 1, no. 26), as this ancient body of water may be named, have left few remnants, other than the streams which flow eastward from the East Humboldt Range to disappear near the base of the mountains. Although it is generally charted as a large body of water, Snowwater Lake (in early years called Eagle Lake) is ephemeral. The name obviously implies that the playa is filled only by spring-melt water, not that it has the purity of snow! There are only a few springs on the terraced slopes between the present lake bed and the mountains.

The tributary streams are reputed by some to contain a native cutthroat trout, but such hearsay evidence is unreliable. No collections were made in these waters. If cutthroats did occur here originally, they are probably now bred out by introduced rainbow (Miller and Alcorn, 1946: 176). The "lake" of course cannot support fish life. With one exception, so far as we could determine, all springs in Clover Valley, as well as in the tributary Independence Valley to the east, are fishless. The one exception is a small spring located at the base of a projecting lava point near the western shore line of Clover Lake. In the pool formed by this spring there dwells a dwarfed and apparently differentiated representative of the type of dace that occurs through the general region. Free (1914*a*) believed that the "Clover group of basins" was tributary to Humboldt River, but we have found no indications, either in the literature or by field observations, that Clover Valley (and Independence Valley) discharged into the Humboldt during Pluvial times. There may well have been an outflow toward the north through the low gap just south of Wells, but if so, the discharge presumably occurred in what we call an "earlier pluvial" period.

27–28.—**Lake Steptoe and Lake Waring**

The now somewhat disrupted hydrographic basin of Steptoe Valley occupies 160 miles of the major structural trough which passes through Ely and extends far across Nevada in a north–south line. A Pluvial lake (map 1, no. 28) in the northern part of the valley was mapped by Russell (1885), but he indicated it as extending several miles too far southward. To reach that far it would have overflowed the cross barrier just above (south of) Currie and would have covered what is now the bed of Goshute Lake, an ephemeral sump basin for the waters from farther south. As demonstrated by Spencer (1917) and by Clark and Riddell (1920) this playa lake is the lowest part of the bed of another Pluvial lake, which Clark and Riddell appropriately named Lake Steptoe (map 1, no. 27). This was a rather extensive body of water, though smaller, much shallower and presumably of briefer existence than the main lake, which lay at a lower elevation to the north. Clark and Riddell gave some indications that a third lake, still smaller and shallower, may have existed for a time above and south of Lake Steptoe.

Confusion exists as to the nomenclature of the main, northern Pluvial lake of Steptoe Valley. It was not specifically designated by Russell (1885), and was apparently first named, as Goshute Lake, by Clark and Riddell (1920). This was an unfortunate choice, for the Recent lake in the same valley which had long borne that name (since Beckwith in 1855 called it "Lake Goshoot") is the remnant of Lake Steptoe. Furthermore the name is preoccupied by "Lake Gosiute," which had been proposed by King (1878) for one stage of the great Eocene lake that laid down the Green River shales, so famous for the contained fish fossils ("Goshoot" and "Gosiute" are earlier, variant spellings of an Indian tribal name). As a substitute for the unacceptable term Lake Goshute of Clark and Riddell, we propose the name, *Pluvial Lake Waring* (map 1, no. 28), to commemorate Gerald A. Waring's notable contributions to Great Basin hydrography.

Lake Steptoe discharged into Lake Waring. In so doing it drained itself almost completely by the downcutting of its outlet through the bedrock cross ridge just south of Currie. The steep-sided canyon is followed by the Nevada Northern Railway. At high-water levels Lake Goshute discharges through this channel (Beckwith, 1855, and recent testimony). The stream was forced into the bedrock by a huge Prepluvial alluvial fan that fills the western part of the valley just above Currie. After Lake Steptoe was drained, its bed above Goshute Lake was occupied by a Pluvial and Postpluvial stream which may be known as *Steptoe River*. The lower part of the channel, now locally known as Steptoe Slough, though generally mapped as Duck Creek and earlier designated as Willow Creek, still carries a considerable flow in wet seasons and of course is subject to desert floods.

Following his practice of finding a discharge for all basins which did not produce large salt deposits, Free (1914*a*) held that Steptoe Valley was occupied by a Lake Bonneville tributary which crossed the Toana Range east of Cobre. We find, however, that the physiographic evidence negates his assumption. The uppermost, very sharp terraces on the two sides of Lake Waring were estimated from altimeter readings to lie about 170 to 180 feet above Shafter, and to reach the valley floor about midway between Shafter and Cobre, which is on the Waring–Bonneville divide (in Nevada near the Utah line). This pass at Cobre is about 140 feet above the level of the highest Waring terrace. There are no obvious Postpluvial disturbances of the terrace levels. The valley slopes gradually downward from its rim at Cobre southward to Shafter and beyond. For the first 9 miles the lowest part of the trough is followed by the Nevada Northern Railway, the track of which has been badly washed out by floods from both sides. There could have been no lake overflow to the northeast, for all of the northernmost part of the valley bottom lay above Lake Waring. Topographic relations in this region are best shown on a map in Lee, Stone, Gale and others (1915). Probably the lowest pass across the Toana Range south of Cobre is Silver Zone Pass, which lies, according to our altimeter readings, about 130 feet above the top lake terrace. Thus our observations, supplemented by information and road-bed profiles

ndly furnished by W. R. Armstrong, Chief Engineer of the Nevada Northern
ailway Company, confirm the general view that Steptoe (Goshute) Valley
as an enclosed basin in Pluvial as well as in Recent times. How the basin
eceived its fish fauna therefore calls for consideration.

Numerous springs in Steptoe Valley, around the edge of the Pluvial lakes
nd in tributaries of Steptoe River, are populated by the peculiar type of
ace of the Ruby–Clover–Steptoe–Spring Valley region. Several of the local
aces show slight to extreme degrees of differentiation, probably Postpluvial.
ne spring, on Murphy Ranch, near the northern end of Steptoe Valley,
ielded Utah chubs (*Gila atraria*), a species widespread in the Bonneville
asin. How this fish reached Steptoe Valley is not yet obvious, though it
as probably introduced by man (Miller and Alcorn, 1946: 182). It is locally
hought that the chubs were brought in a few years ago, along with a re-
tocking of trout. Despite the fact that we cannot trace the origin of this
tock with certainty, because the fish look somewhat unlike those of any
opulation of *atraria* that we have seen in the Bonneville Basin, we do not
egard these fish as a distinct race nor do we interpret this occurrence as
vidence for Free's view that Steptoe Valley was tributary to Lake Bonne-
ille.

The most plausible source for the native *Rhinichthys*-like fishes of Step-
oe Valley is Butte Valley of the Pluvial Lake Franklin system. A water con-
ection between Butte and Steptoe valleys may have existed over an interven-
ng saddle, Goshute Pass, the highest point of which lies 11.8 miles by high-
ay northwest of Currie. Here slight drainage channels from the mountain
o the southwest flow over the nearly flat alluvial slope perpendicularly to a
efinite, though small and shallow valley, which, oddly, crosses over the
early flat divide between the two basins. Pluvial streams, possibly large and
ermanent enough to have harbored dace, would presumably have wandered
ack and forth across the fan, swinging the drainage now toward Butte Val-
ey, now toward Steptoe. The little valley crossing the divide looks like a
tream channel, but if so, it can hardly represent a Pluvial channel since the
ivide lies far above the highest Pluvial lake terraces on either side. The
rough may have been formed by faulting. We cannot subscribe to Free's
914*a*) impossible view that Ruby Valley discharged over Goshute Pass,
ther as a stream or as a lake overflow, during what Free called the "Lahon-
n period." If or when Lake Franklin of Ruby Valley overflowed it must
ave discharged into Clover Valley to the north (p. 52), because the lowest
oint in the rim of the Ruby basin is in Wells Fargo Canyon.

The structural trough occupied in part by Steptoe Valley is continued
outhward into Cave Valley. That basin is barely disrupted from the valley
the Pluvial White River, which flowed into the Colorado River (p. 96). The
ivide between Steptoe and Cave valleys, however, is far too high and sharp
to suggest any water connections, and no fish life was found in Cave Valley.

29.—**Antelope Lake**

A now dry arm of Steptoe Valley extends up Antelope Valley, contiguous to the Bonneville divide. Various maps of the Pluvial lakes properly indicate that a bay of Lake Waring extended for some distance into this valley. However, the head of Antelope Valley (in the vicinity of Tippett Station on the old stage route) comprises the wholly circumscribed basin of an ancient lake (map 1, no. 29), which Jones (1940) named Antelope Lake. This lake was discovered and first mapped by Clark and Riddell (1920), but they drew the bed too large and too elongate. The lake was oval in outline and lay entirely south of Lat. 40° N. We have sketched the outline from field observations though we did not make a detailed survey.

There has been some confusion in regard to the drainage relations between the waters in this basin and those of Deep Creek Valley of the Bonneville basin, lying just to the eastward. On his map of the Bonneville level of Lake Bonneville, contradicting his general map of Pleistocene lakes, Jones (1940) included the Tippett Basin, which held Pluvial Antelope Lake, as a part of what he labelled "Deep Creek Bay" of Lake Bonneville. Alluvial saddles well above the highest lake-shore features on either side, however, disconnect Tippett Basin from Deep Creek Valley, as well as from the main part of Antelope Valley. Gilbert and Howell's "Restored Outline of Lake Bonneville" (no. 12 of Atlas Sheets to accompany Rept. Geogr. and Geol. Sur. W. 100th Mer., 3, 1875) also showed a wide arm of Lake Bonneville extending far up Deep Creek Valley, but Gilbert (1890) later correctly indicated that the Bonneville shore line penetrated narrowly only the lower part of that valley. It is true that the main portion of the Deep Creek basin contains lacustrine beds, but these are believed to be Pliocene (King, 1878; Spencer, 1917) and seem to have been laid down in a separate lake above the barrier of lava cross hills, through which Deep Creek is now entrenched. The canyon was apparently Prepluvial in origin for the Bonneville terrace extends into it and the lower (northern) part of Deep Creek Valley, between 5000 and 5200 feet elevation (U. S. G. S., Gold Hill Quadrangle), has been indicated as occupied by the Deep Creek bay of Lake Bonneville at its highest stage. Incidentally, "Gandy Cut-off," shown by dotted lines on some of Jones's maps, as a connection between "Deep Creek Bay" and Snake Bay of Lake Bonneville, covers a ridge that rises far above the highest Bonneville terrace.

There is some live spring water in the basin of Pluvial Antelope Lake, but no indication of native fish life. This is unfortunate, as it is not clear whether this basin should be aligned with the group under consideration or as a disjunct unit of the Bonneville complex.

30.—**Spring Lake**

Adjacent to Tippett basin, and intervening between and paralleling the drainages of Steptoe Valley and of Snake Valley (which is hydrographically and faunistically a part of the Bonneville basin), lies the elongate north–south trough of another Pluvial lake (map 1, no. 30). This deep basin, one of the several "Spring Valleys" of Nevada, lies near the Utah border between Shell Creek Range and Snake Range, which includes Wheeler Peak. The Pluvial lake which formed here was moderately large and rather deep, especially toward the south. It was first mapped by Clark and Riddell (1920), and apparently first named, as "Spring Lake," by Jones (1940). This author suggested that the shore features of this lake, as well as those of Lake Waring and Antelope Lake, may have been confused by some geologists with those of Lake Bonneville, but we have not encountered the basis for such suspected confusion. Most of the creeks and springs in the valley seem to be devoid of native fish life, and Cope and Yarrow (1875) marvelled at the lack of fish in this valley (then named Schell Creek Valley). However, we collected two species of fish in Spring Creek, which flows into Spring Valley from the north, and since our field work was done we have heard that minor springs forming a series on the east side of the valley contain small fish. One of the species we collected, a rare one, is a new sucker, with characters that line it up best with a Bonneville, or possibly a Colorado species. The other fish taken is a spring dace, very much like the highly distinctive types that also occur in Steptoe, Butte, and Ruby valleys. The most plausible source of the dace would seem to be Steptoe Valley, but we saw no indications of any sort of hydrographic connection across the high divide. The physiographic evidence as to former discharge connections of Spring Valley waters is also inconclusive. Contrary to Free's (1914*a*) idea, the two lowest divides lie south of Wheeler Peak, and lead respectively east toward Snake Valley of the Bonneville system, and south to Duck (or Lake) Valley, at the western headwaters of Pluvial Carpenter River, a Colorado tributary (p. 98). Both of these divides lie well above the terraces of Pluvial Spring Lake, and the characters of the dace of Spring Valley do not favor either a Recent or a Pluvial connection with either Lake Bonneville or Carpenter River. There are Utah chubs (*Gila atraria*) in Spring Valley (in Shoshone Spring), but we ascertained that this Bonneville species was introduced here by Mormon settlers. The trout in the Shell Creek Range, on the western slope of Spring Valley, are definitely reported to have been brought in, probably first from Trout Creek, Utah (Miller and Alcorn, 1946: 177). As a result of his survey in 1869 Wheeler (1875: 54), remarked on the lack of fish in the mountain streams of the Great Basin, except in the Humboldt Range and to the east of Snake Range.

31–32.—**Lake in Long Valley and Lake Jake**

Two other basins of independent interior drainage in Nevada are included in the group under treatment, although they appear to be fishless and one of them might more logically be included among the basins disconnected from the White River system. These valleys, Long and Jakes, occupy in series an intermountain trough that connects Ruby Valley with the upper end of the drainage basin of Pluvial White River of the Colorado system (pp. 96–98). This trough is crossed by three divides, which though low appear to have separated these minor basins from one another and from the fish-containing valleys to the north and to the south during Pluvial as well as Recent times. Some maps wrongly show Long and Jakes valleys as separated by a high range (Butte Range) and indicate Jakes and Butte valleys as forming a common trough. On the same maps the name White Sage Valley is used in place of Jakes Valley, which designation is erroneously given for the upper end of White River Valley.

Free (1914*a*) indicated that Long Valley (his "Murray Valley") was tributary to Ruby Valley in the Pluvial period, but on the basis of local testimony we question this view. However, since no pertinent physiographic details have been published, and since we did not investigate the divide, we are not yet certain that Long Valley was disconnected from Pluvial Lake Franklin. Long Valley contains a dry lake (map 1, no. 31) and should be examined for evidences of a Pluvial lake. Its one valley-bottom spring of consequence, "Long Valley Slough," as well as the few mountain springs in the drainage basin, is definitely indicated by well-informed local cattlemen to be totally fishless.

Jakes Valley is a rather deeply enclosed basin, lying west of Egan Range and east of White Pine Mountains. It is separated by canyon-gutted mountains of moderate height from Long Valley to the north and by low mountains and high alluvial slopes from White River Valley to the south. The valley obviously had no Pluvial discharge. If an "earlier pluvial" outlet connected this basin with any other, the flow would have been southward into

White River. A trout stream, Illipah Creek, permanently reaches the valley floor, but the entire basin is wholly devoid of native fish life (Miller and Alcorn, 1946: 177–178). Toward the south the bottom of the valley is a white-sage flat about 15 miles in the longer diameter. This flat is said to be surrounded by a succession of beach lines. Across the southern part of the presumed lake bed there is reported to be a long bar of somewhat cemented rounded stones, which, after the filling of one gulley, has served as a reservoir dam. These features almost certainly indicate the former presence of a lake (map 1, no. 32), which tentatively may be called *Pluvial Lake Jake,* after the current name of the valley, which in turn was named for "Dutch Jake," the first settler.

LAKES NORTH OF LAHONTAN SYSTEM

Toward the east the upper tributaries of the Lahontan system are set apart from Columbia River waters by mountain divides, but toward the west these great systems are separated by an extension of the Great Basin in which the terrain is broken into numerous depressions, each of which contained an isolated Pluvial lake. Four other lakes in this region (separately discussed later) are each thought to have had an outlet: Pluvial Lake Malheur and Fort Rock Lake in Oregon almost certainly drained into the Columbia system; Goose Lake in Oregon and California still occasionally overflows into the Sacramento system; and Klamath Lake in the same states has discharged since Pluvial times into the Pacific Ocean. The fish faunas of these enclosed and outlet "basins of the lava plateau" (Free, 1914*a*) offer evidence of varying value in the interpretation of their hydrographic history.

On his modification of Meinzer's map of Pleistocene lakes, Nolan (1943) indicated that a large lake existed in the Owyhee River drainage basin of southeastern Oregon, east of the Alvord Basin. In reply to a somewhat bewildered query Noland wrote that this lake "was born some time between the submission of my manuscript copy of Mr. Meinzer's map, and publication, —and I strongly suspect that it represents a blot by the draftsman." Let us hope that it was still-born.

With the exception of Madeline Plains all of the lake basins discussed in this section have been regarded as independent of the Lahontan system.

33.—Lake Madeline

Except for doubts raised by Free (1914*a*), the extensive flat-bottomed Madeline Plains have been treated as a part of the Lahontan drainage basin, ever since Russell (1884) wrote that the Pluvial lake (map 1, no. 33) in this basin rose until the "river formed by the discharge of this lake flowed southward across the lava-overflow" into a tributary of Honey Lake. Repeated altimeter readings in 1942, however, indicated that the lowest points along the flat top of the massive lava barrier are about 30 feet higher than the strongly marked uppermost terrace (Fig. 13) of *Pluvial Lake Madeline* (as we may call the lake). The south side of the barrier, however, is entrenched by canyons far too deep to be plausibly explained as having been carved by rain-fed drainage off the barrier. An "earlier pluvial" overflow across the lava could have produced this topographic feature, but we are inclined to the view that the canyon-cutting waters came from Lake Madeline by seepage through fissures in the lava dam. That there are still large undersurface channels through the lava is demonstrated by the presence over the level parts of the lava surface of innumerable shallow sinkholes, in which the lava boul-

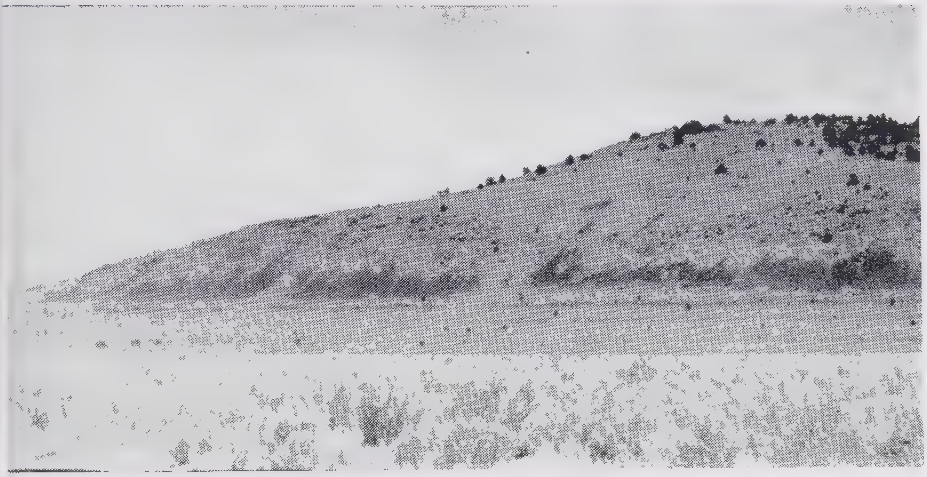

Fig. 13. Terraces of Lake Madeline, south of Madeline, California. The highest and strongest terrace represents a seepage outlet stage.

ders have been washed clean of fine sediment, obviously by downflowing water. Pluvial Lake Madeline presumably rose until the seepage outflow plus evaporation balanced the inflow.

Because the Madeline basin may be assumed to have had such a seepage discharge into Honey Lake, physiographers may still include it in the Lahontan drainage area, but since fish would not likely have passed with the water through fissures in the lava the basin will be regarded by ichthyologists as an independent system of interior drainage. Fish may have gotten into Madeline waters during an "earlier pluvial" overflow, but the canyons to the southward are too steep to be regarded as a very plausible route of invasion for fish.

An apparent stream capture provides a more probable explanation for the presence of fish in the Madeline basin. A stream that flows westward from Clark Valley to the vicinity of Tule Marsh (see Alturas Quadrangle, U.S.G.S.) presumably once continued to Madeline Plains, but seemingly became diverted into the South Fork of the Pit River by the back-cutting of the West Valley Canyon. The creek has now been diverted back into the Tule Marsh basin to fill a reservoir, from which the water is drawn for irrigation in the north end of Madeline Plains. During the beheading of the creek, on the marshy flat, there would no doubt have been ample opportunity for the movement of dace from the Pit River division of the Sacramento system into the basin of Lake Madeline. The transfer presumably took place during Pluvial time, when there was enough water to disperse fish to springs and short creeks that are now separated by miles of dry plains. The only species now occurring on the Madeline Plains is a dace, *Rhinichthys osculus,* of a subspecies apparently indistinguishable from the local form of the Pit River system.

Not wholly in agreement with a statement by Free (1914*a*), we determined that Grasshopper Valley forms an integral part of the flat Madeline Plains, though the connection with the main part of the basin was a very narrow strait of Lake Madeline. Grasshopper Valley contains the same type of *Rhinichthys osculus* that occurs in the main part of Madeline Plains. Rutter (1903) erred, we think, when he identified the *Rhinichthys* of Grasshopper Valley with that of the Lahontan and expressed the view that "Grasshopper Plains" was at one time tributary to Lake Lahontan.

34.—Lakes in Alvord Basin

The easternmost of the lake systems north of the Lahontan basin drained into a large sump, Pluvial Lake Alvord (map 1, no. 34), located chiefly in Oregon, just east of Pueblo Mountains and the mighty escarpment of Steens Mountains (Smith, 1927; Fuller, 1931). This lake was named by Smith and Young (1926). Thousand Creek and its tributary Virgin Creek, in northern Nevada, discharged into the southern part of the ancient lake. This basin also contained a Pliocene lake and a Miocene lake (Merriam: 1910, 1911, 1917).

Our ichthyological findings strikingly confirm the Pluvial history of the Alvord basin, as this was worked out by Russell (1884), Waring (1909) and Free (1914*a*). The most remarkable fish in the basin is a chub that we have tentatively referred to *Siphateles,* though it is so distinct that it may be set apart in a new genus. After first finding this fish in several places in the Alvord Desert region in Oregon, we hypothesized that it should occur in the Thousand Creek system in Nevada, went there, and located it again. As this very distinct species occurs nowhere else it furnishes convincing evidence, firstly of the former extent and continuity of the Lake Alvord system, and secondly of the long isolation of this system, presumably since Prepluvial time (Hubbs and Miller, 1942). The *Siphateles* is found chiefly in the meadow waters, and, as a slightly different form, in the hot mineral waters of Borax Lake—a spring pond which has built up its circular rim so that it lies, fantastically, well above the general level of the Alvord playa. Several creeks in the basin contain native cutthroat trout, which show local peculiarities correlated with their isolation. Little credence, therefore, is placed on local rumors that these trout were introduced.

The fish evidence, and we believe the physiographic evidence, is out of agreement with Free's (1914*a*) guess that Lake Alvord may have drained into Malheur River and with Smith and Young's (1926) suggestion that this lake may have discharged "via Sand Gap and Whitehorse Valley into the Jordan Valley, and thence down the Owyhee to the Snake." According to Russell (1903*b*) the rim of the Whitehorse basin is everywhere rather high and distinct, except on the side adjacent to Alvord Valley. There may of course have been an "earlier pluvial" discharge into Jordan Valley, but in Pluvial times, as now during floods, Whitehorse Valley was apparently connected only with Lake Alvord. It was probably flooded by an arm of that lake at the highest water level, and at other times was undoubtedly tributary to the lake.

Several very small lake-containing basins, in the same structural trough, lie north of the Alvord playa, as Russell (1884, 1903*a*–*b*) and Waring (1909) indicated. Two of these, Lake Mann (no. 34*a*) and Lake Juniper (no. 34*b*), have each been indicated as the site of an enclosed Pluvial lake, though Free wrote that they were flooded by Lake Alvord (it will be noticed that Free, 1914*a*, confused this Juniper Lake with the pond of the same name near Warner Lake). No native fish was found in these now disjunct basins, although at high levels they may have been connected with Lake Alvord. When we passed by them in the drought year of 1934, Juniper Lake, "Dime" (Ten-cent) Lake, and other waters of the region were dry.

35.—**Summit Lake**

So named because it lies in a small basin on the summit between Virgin Creek of the Alvord system to the north and Soldier Creek of the Lahontan drainage to the south, Summit Lake (map 1, no. 35) in northern Nevada has generally been neglected in studies of the hydrography and ichthyology of the Great Basin. This lake and its tributary, Snow Creek, contain only one species of fish—a cutthroat trout that may be slightly differentiated. Since cutthroats occur in Virgin Creek, and in Pluvial times presumably occurred in the precipitous upper waters of Soldier Creek, the fish evidence is noncommittal as to the former connections of Summit Lake. But since there is a low point in the rim between the lake and Soldier Creek we may assume that the lake once discharged into the deep and steep canyon leading toward Soldier Meadows. Free (1914*a*), however, definitely erred in indicating that such a connection still exists. Physiographic evidence suggests that this connection was either very temporary or, more probably, of an "earlier pluvial" period. There are definite indications of a Pluvial Summit Lake, a little deeper and of considerably greater expanse than the Recent lake (the outline as shown on our map is an approximation from field observations). The lake, however, was not deep enough to have overflowed, even though the notch in the southern rim of the basin is only about 40 feet above the lake level (according to altimeter readings). That the lake remains nearly fresh is no conclusive argument against the theory of its long existence, for it is deep and its salts may be eliminated by underground flow, as Hutchinson (1937) assumed they are from Soda Lake, near Fallon, Nevada. Summit Lake may well be the source of the hot springs in Soldier Meadows, far below. Such an underground outlet might also explain why Summit Lake failed to rise quite high enough to overflow in Pluvial times. Or at a higher level the lake water, like that of Lake Madeline (p. 58), may have seeped through the rock wall to feed the canyon-entrenched creek to the south. The lay of the land explains why no other fish occur in the Summit Lake basin, for only trout would be expected to have occurred in the adjacent headwaters, either to the south or to the north. It is even possible that the trout of Summit Lake and Snow Creek was introduced, for there was an army camp in the basin (now an Indian Reserve) and J. R. Alcorn (of Fallon, Nevada) tells us of reports that trout were introduced about 40 years ago.

35*a*–36.—**Lake Catlow and Guano Lake**

Geologists Russell (1884) and Waring (1909) and anthropologist Cressman (1942, 1946) have described Pluvial Lake Catlow and the modern remnants of its system, and we too have examined these waters, which lie between the basin of Lake Alvord and that of Guano Lake. Lake Catlow probably once drained across a low divide into the Malheur basin, and by this connection could have derived its one native fish. Since the divide is higher than the highest recorded Catlow terrace (Waring, 1909; Cressman, 1942; Antevs and Smith, personal communications) the overflow was probably either very temporary or, more probably, was of some "earlier pluvial" period. Free (1914*a*) suggested that the terraces are relatively recent and that there may have been a Lahontan discharge. It seems more plausible, however, to assume that the Catlow and Lahontan terraces were contemporary, or nearly so, and that any overflow which may have existed was of much earlier date.

The fact that the endemic form of *Siphateles* in the springs and creeks of Catlow basin is less distinct than is the species of the Alvord basin to the south and east indicates that Catlow Valley has been isolated for a briefer period than the Alvord basin has been, but the rather distinct features of the Catlow chub suggest that Catlow Valley has been isolated longer than most other valleys in southeastern Oregon (Hubbs and Miller, 1942). According to persistent local statements some kind of chub, probably the same or very closely related, abounded prior to the 1934 drought in Rock Creek, which flows from the north face of Hart Mountain eastward to a playa on the bed of Lake Catlow; but we were unable to obtain any specimens in this creek in 1939, although we followed and fished it from its mouth very nearly to its source (where only trout were caught). Local testimony definitely indicates that the trout of the tributaries of Catlow Valley have been introduced. Native cutthroat trout were first brought in from Trout Creek of the Alvord system, but these have now been displaced by later plantings of rainbow trout.

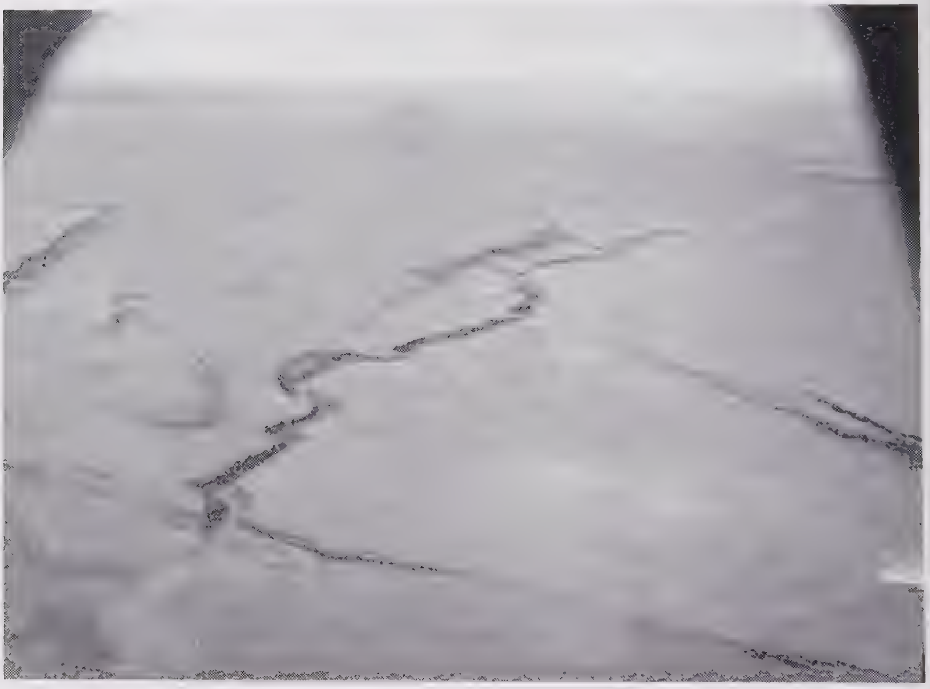

Fig. 14. Lava channel of Pluvial Guano River, Oregon, looking northward and downstream. Tributary dry washes indicate the direction of flow. Air photograph contributed by William E. Fuller.

On the lava plains of southern Oregon and northern Nevada there lies a drainage system which is now mostly dry, but which in Pluvial times must have contained several live creeks draining into the basin of Guano Valley. According to the data of Russell (1884) Pluvial Guano Lake (map 1, no. 36) lay in an enclosed basin, separated by a definite rim from all surrounding waters: Lake Alvord to the east, Lake Lahontan to the south, Lake Meinzer and Lake Warner to the west and Lake Catlow to the north and east. According to Waring's topographic map (1909) the Catlow basin rises westward to contours that are higher than the indicated elevation of the Recent bed of Guano

Lake. Cressman (1936 and personal communications), however, regards this portion of the survey as incorrect. Disagreeing with earlier authorities (other than Free, whose opinion was only a guess), Cressman feels sure that Guano Lake, a shallow body of water, discharged northward through the long, deep channel of "Guano Slough" (Guano Canyon) across a downward-sloping lava plateau into Lake Catlow. Fuller and Waters (1929) claimed on the contrary that the slope of this canyon is to the southward and that it represents a rejuvenation of the drainage caused by a very recent upthrust. A re-examination of the photographs of the drainage used by Cressman and by Fuller and Waters to illustrate their conflicting views, and of other excellent photographs kindly provided by Dr. Cressman and Dr. Fuller (Fig. 14), and additional supporting evidence, leads us to agree with Cressman that the drainage of Guano Canyon slopes toward the north and that this deep trench in the lava was carved by the discharge of ancient Guano Lake. The stream that once occupied this now generally dry canyon may be known as *Guano River*. This was obviously a Pluvial stream but may well have originated during an "earlier pluvial" period.

Two of the headwater spring-fed tributaries of the Guano system, near the Nevada–Oregon line, contain chubs (*Siphateles*) that provide evidence on these problems of former drainage. Although living only a few miles apart they are isolated, because the connecting stream beds are dry except in floods, which, we have repeatedly seen, have little effect on the distribution of desert fishes. The two stocks are racially and perhaps subspecifically distinct. Contrary to our earlier opinion (Hubbs and Miller, 1942), based on preliminary examination, these Guano-basin chubs are very similar to the rather distinctive *Siphateles* which inhabits the springs of Catlow Valley. This similarity in the fishes is in harmony with the view that Pluvial Guano Lake discharged into Lake Catlow. Reliable local testimony indicates that chubs were caught in Guano Creek up to 1934, but in 1939 we did not investigate this creek, which during the dry season consists largely of disconnected pools in the upper parts and is completely dry in its lower course.

37.—Lake Meinzer

We have made a study of the rather large Pluvial lake (map 1, no. 37) of Long Valley, in extreme northwestern Nevada, checking Russell's approximately accurate maps (1884 and 1885) of this lake, and confirming his view that the lake attained no outlet, at the level of the well-marked highest terrace. The pass leading north toward Coleman Valley seems to be lower than any of the depressions in the rim between Long Valley and the three drainages to the southward (the Nevada headwaters of the Guano system; the High Rock tributaries of the Lahontan system; the Wall Canyon tributaries of the Surprise system). With obviously inadequate data Free (1914*a*) inclined to the belief that Long Valley discharged into the Duck Flat division of Lake Surprise. The pass toward Coleman Valley was found by altimeter readings to be about 80 feet above the highest terrace. Any outflow in that direction was either very temporary or, more likely, of an "earlier pluvial" age.

The ancient lake which left its signs clearly imprinted on the slopes of Long Valley may be named *Pluvial Lake Meinzer*, to commemorate the outstanding contributions which Oscar E. Meinzer has made to the Pleistocene and Recent hydrography of the Great Basin. The deep waters of Lake Meinzer extended from 41° 20′ to 41° 55′ N. Lat. and from 119° 30′ to 119° 53′ W. Long. Free's map (1914*a*) of the Long Valley basin is a travesty. It shows this drainage unit as including Coleman Valley, which was covered by a bay of Lake Warner, but indicates that Massacre Lakes are in the Lahontan system. These lakes actually lie on the floor of Lake Meinzer.

After some fruitless search we recently located, in Vya Spring, a fish population in the now much desiccated Long Valley basin. Unfortunately it is a *Rhinichthys,* of a type which is generally distributed in contiguous portions of Nevada, California and Oregon, and which shows only obscure and confusing evidence of former lake connections. It is perhaps most like a subspecies in Coleman Valley of the Warner system just to the north. To our distress, however, it is also much like forms occurring in Surprise Valley to the west and in the High Rock system (of the Lahontan complex) to the southeast.

38.—**Lake Surprise**

First mapped by Israel Cook Russell in 1884 and named by Richard Joel Russell forty-three years later (1927*b*), Pluvial Lake Surprise (map 1, no. 38), in the extreme northeastern corner of California, likewise seems never to have overflowed in Pluvial times. It was set off by high divides from the waters of Goose Lake, Pit River and Madeline Plains to the west, and from Long Valley (Lake Meinzer) and the High Rock waters (Lake Lahontan drainage) to the east. It was separated by lower but definite passes from Cowhead Lake (map 1, no. 40) of the Warner system, to the north, and from the Lahontan system to the south. An outlet to the south through Buffalo Canyon has been claimed (Russell, 1927*b*; Jones, 1940), but according to our altimeter readings the pass is 310 feet above the level of the highest terrace of Lake Surprise, at the south side of Duck Flat. Russell further erred in indicating that "Buffalo Meadows," in the course of the alleged outlet, constitute a broad channel. Actually, these hay meadows form narrow canyon-bottom strips, mostly in a side canyon. He was also in error in stating that Lake Surprise barely overflowed into Duck Flat. In agreement with this error the Long Valley Quadrangle (U. S. G. S.) indicates that a stream divide separates the two basins, but this map is notoriously unreliable in general and is definitely wrong in this particular. When in flood Wall Canyon Creek has two distributaries, one of which feeds Duck Lake while the other flows north through the intervening canyon into Surprise Valley. The arroyo beds are continuous and the direction of flow is obvious from local testimony as well as from field observations. At its higher levels Lake Surprise flooded Duck Flat as well as Surprise Valley, for the well-defined uppermost terrace is higher than the floor of the intervening canyon, which was occupied by a narrow strait, in and just above which fine tufa formations were laid down, as Russell (1884: 461) stated. A second low pass from Duck Flat to the south, toward Squaw Creek (also of the Lahontan system), is still higher. The pass to the north, toward Cowhead Lake, is probably at least as high as that toward Buffalo Canyon, and is visibly higher than the highest terraces of Lake Surprise.

Whether an "earlier pluvial" outlet flowed to the north or to the south is not certain, and the fish evidence, unhappily, is not very conclusive. In the Surprise system there are many widely scattered populations of dace (*Rhinichthys*) and an endemic sucker (*Catostomus*), now confined to the tributary Wall Canyon, but both species are closely related to forms occurring in the Warner system as well as in the Lahontan basin. They may indicate "earlier pluvial" drainage relations at different periods in both directions.

39–40.—**Lake Warner and Cowhead Lake**

The first to be considered of the "Oregon Lakes system" of Snyder (1908*b*) is the complex of Warner Valley (Fig. 15), the now disrupted portions of Pluvial Lake Warner (map 1, no. 39), which was described and mapped by Russell (1881, 1885), Snyder (1908*b*), and Waring (1908, 1909). These authors indicated that Lake Warner had no outlet at its highest Pluvial level. Van Winkle (1914) thought that it discharged into Lake Malheur, but in a footnote presented conflicting evidence. In our opinion the physiographic data provisionally call for an "earlier pluvial" outflow into Malheur River. The fish evidence is conflicting. The Warner basin contains a sucker (*Catostomus*) that may be related to a species of the Columbia, of the Surprise, of the Lahontan or of the Sacramento system; an endemic minnow referred to the Sacramento genus *Hesperoleucus* (the genus is also represented in tributaries of Goose Lake to the westward and may have entered Warner Valley by stream capture); two endemic subspecies of the chub *Siphateles obesus* and three of the dace *Rhinichthys osculus,* both of which are of too wide occurrence in surrounding basins to be of very critical value in hydrographic interpretations; and probably a trout, also of little geographic significance. The high degree of endemism is in agreement with the idea that the system has been isolated since before Pluvial time. One of the *Rhinichthys* subspecies occurs in Coleman Valley, which is now wholly separated from Warner Lake, but which, according to published maps and our altimeter readings, was occupied by a deep bay of Pluvial Lake Warner. There is a local form of the *Siphateles* and one of the *Rhinichthys* in Cowhead Lake (map 1, no. 40),

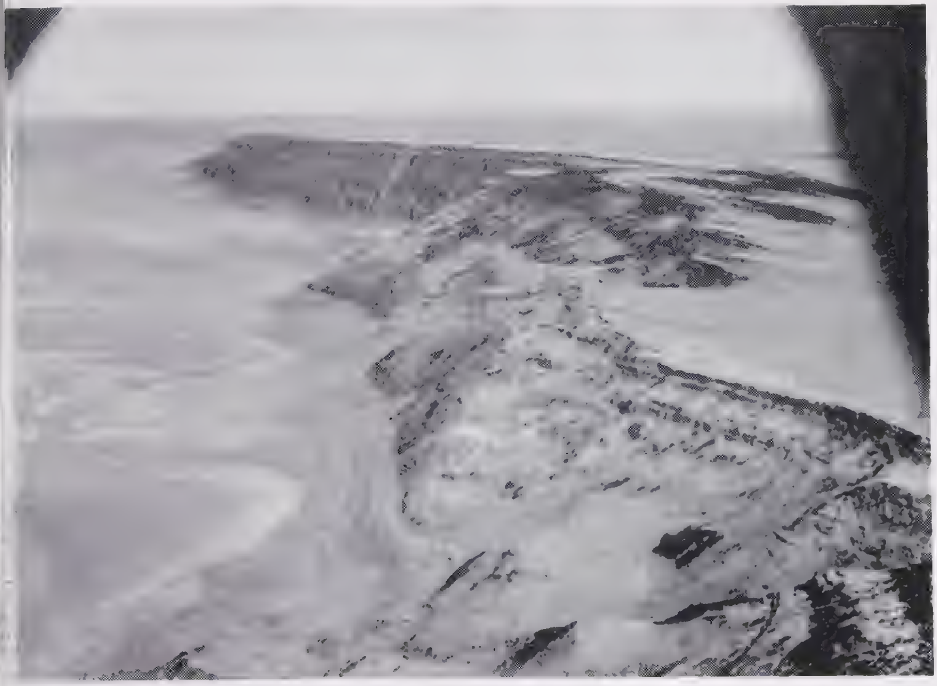

Fig. 15. Warner Lakes and Warner Mountain, Oregon. Pluvial Lake Warner covered the floor of the valley to the height of the terraces along the bold escarpment. Photograph contributed by William E. Fuller.

which lies on the pass between Warner Valley and Surprise Valley but drains (at high-water levels) into Warner Lake (Free, 1914*a*, wrongly included Cowhead Lake in the Surprise basin, into which he thought it formerly overflowed). We therefore again find evidence of a moderate amount of speciation, hastened by isolation, since Pluvial time. Cowhead Lake probably existed during the Pluvial periods, but no study has been made of its terraces.

Juniper Lake, an isolated pond just west of Adel, in the Warner basin, was indicated by Free (1914*a*) to have been a separate Pleistocene lake, but it is clear that he came to this conclusion through a confusion of this pond with the Juniper Lake (p. 60) that lies just north of Lake Alvord.

40*a*.—**Alkali Lake**

As indicated by Waring's (1908) map of its lacustrine deposits, the Pluvial lake called "Quaternary Alkali Lake" by Hubbs (1941*a*) extends approximately from 42° 47′ to 43° 13′ N. Lat. and from 119° 57′ to 120° 12′ W. Long. According to Waring it was nearly 100 square miles in area and 275 feet deep, yet it was omitted from Meinzer's 1922 summary and map of the Pleistocene lakes of the Basin-and-Range Province, as well as from all subsequent reproductions and modifications of that map. Free (1914*a*) also described and figured the bed and terraces of ancient Alkali Lake. As was pointed out in 1941 the only remnant of the fish life of this enclosed basin and the only remaining permanent water are confined to one small spring (Fig. 16). The fish is a form of *Siphateles obesus,* very closely related to the subspecies that inhabit the present fragments of Pluvial lakes Chewaucan and Fort Rock, to the southwest, west and northwest. Van Winkle (1914) thought that Alkali Lake may have drained into the Chewaucan basin. Snyder (1908*b* and 1917*a*) mentioned the fish but gave neither it nor the ancient lake a distinct name. The fish will require further study. Pluvial Alkali Lake is the designation we plan to use for the lake.

40*b*.—**Lake Chewaucan**

That the waters of Summer Lake, Chewaucan Marsh and Abert Lake are remnants of a rather large, wholly enclosed Pluvial lake was adequately demonstrated by Russell in 1884 and by Waring in 1908. This ancient lake,

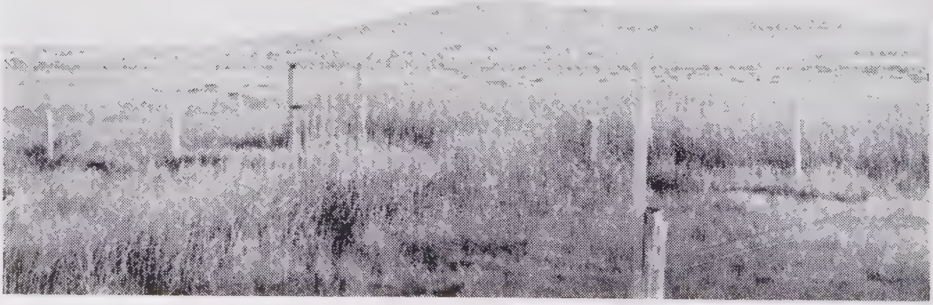

Fig. 16. Alkali Spring and terraces of Pluvial Alkali Lake, Oregon. This spring contains the only remaining water and the only fish in the basin of the ancient lake.

which has been named Lake Chewaucan by Huntington (1925), extended in broad "U" from a point near 42° 45′ N. Lat. and 120° 30′ W. Long., with extreme points about 43 miles apart. At the earlier Pluvial stage Lake Chewaucan was 350 feet higher than Summer Lake is now, according to Allison (1946: 64). At the later Pluvial, or Provo, stage, called "pluvial Winter Lake" by Allison, the level was estimated by this author to lie 210 feet above the level of Summer Lake. For the very low intermediate stage he (1945) added the name "Ana Lake." (See p. 22.)

Except for native trout (Cope, 1883), which very probably have been bred out by hybridization with the introduced rainbow trout, and for dace of the species *Rhinichthys osculus* (of uncertain geographic significance), the only remaining fishes of this once vast water are chubs (*Siphateles obesus*). The chubs belong to a group which is widespread in all adjacent lake basins (Alkali, Warner, Goose, Klamath, and Fort Rock). This is a lake and channel type, which must have been widespread and more or less uniform throughout Lake Chewaucan. Isolation since Pluvial times, however, has permitted the racial or subspecific differentiation of the three remnant local stocks, namely those of the northwest side of Summer Lake, those of the Chewaucan River drainage, and those of XL Spring at the north end of Abert Lake. These comprise nearly all of the remaining habitable areas of fresh water.

Summary on "Oregon Lake System"

Largely on the basis of the ichthyological evidence Cope (1883) predicted that it would be shown that the ancient lakes now called Warner, Chewaucan and Fort Rock, and probably Malheur also, are parts of a vast "Oregon Lake," and that this lake might have been connected with the great extinct lake of Nevada. He further hypothesized that Goose Lake and the Klamath lakes formed "another series, characterized by several points of resemblance in their fish faunae. Whether they were connected, forming a single body, at an earlier geological period, is not yet known." Snyder (1908*b*) called these waters the "Oregon Lakes" but recognized the faunal and hydrographic distinctness of Malheur Lake as well as of Goose Lake and of the Klamath lakes, and since then Allison (1940 and personal communication) has indicated that Fort Rock Lake (p. 73) probably discharged into the Columbia River system. "The basins of the other lakes," Snyder wrote, "are completely and widely isolated from any system having connection with the ocean. Although little appears to be known of their geological history, they may for the present be regarded as unconnected parts of what may be termed the Oregon lake system." The fish evidence calls for some connection from these basins of internal drainage to some system or systems that are connected with the ocean, but just what linkages existed and at what time remains to be learned. There is certainly no evidence for a Pluvial lake approaching the extent of Cope's theoretical "Oregon Lake." Nor is there proof that a really major Pluvial lake existed in the Klamath basin.

41.—KLAMATH RIVER SYSTEM

In general the interior drainage has been increasing in area, as additional basins have been cut off from connection with the sea. Disrupted portions of the Sacramento, Columbia and Colorado river systems will be discussed in turn, but before so doing we comment on the fish fauna of a system (map 1, no. 41) which, according to geological and ichthyological evidence, was formerly a part of the interior basin but now flows out to the ocean.

During Pluvial times, according to Russell (1884) and others, the basin of Klamath Lake (no. 41*a*) filled high enough to discharge across its southern rim into Klamath River, and the rim has been cut so deeply that the outlet has persisted to the present, despite the decreased inflow into the basin. Just when these events took place is not clear from any evidence available to us: the palehydrography of the Klamath basin remains to be written. According to our own hasty examination and to advice received personally from Prof. Ira S. Allison, there are no clear-cut terraces or other shore features to indicate that any of the Klamath basin lakes or marshes had, during the last Pluvial periods, a water surface as much as 50 feet higher than the present level.

Remains of large, presumably sea-run salmon in the diatomaceous deposits on Lost River, Oregon (Jordan, 1907) and from the older deposits of Lower Klamath Lake, as reported by Cressman (1942), indicate that Klamath basin had attained its outlet when these lake beds were laid down. The 4 fish bones from Lower Klamath Lake, recorded by Cressman, and kindly referred to us by him, include in addition to salmon remains, the operculum of a large sucker, presumably *Chasmistes*. Another operculum thought to be referable to the same genus came from Recent deposits of this lake. More fossil and semi-fossil material from the region may prove of great help in deciphering the lacustrine history of the Klamath area.

The relationships of the comparatively rich and diverse present-day fish fauna of the Klamath River system harmonize with geological suppositions as to the hydrographic history of the basin. Included are a number of elements related to those of the Great Basin (Gilbert, 1898; Snyder, 1908*c*). Chief among these are the lake suckers: 3 described species of *Chasmistes* and a related form referred to an endemic genus *Deltistes* (Cope, 1879*b*, 1883; Seale, 1896; Gilbert, 1898; Evermann and Meek, 1898). These are comparable among living forms only with *Chasmistes liorus* of Utah Lake (Bonneville) and *C. cujus* of Pyramid Lake (Lahontan). The strength of this tie-in is weakened, however, by the preliminary identification as *Chasmistes* of sucker remains from the beds of Pluvial Fort Rock Lake, which is now thought to have discharged into the Columbia River system (p. 73). An endemic minnow species, *Gila caerulea,* is perhaps remotely related to the Utah chub or to a species of the Sacramento system; its distinctiveness has been emphasized recently by assigning it to a distinct subgenus, *Klamathella* (Miller, 1945*b*). *Catostomus snyderi* and the local representatives of *Rhinichthys* may be related to the forms of the Great Basin or to those of the Columbia or the Sacramento drainage basins.

The native cutthroat trout may be of Great Basin origin or it may be a Glacial relict. The Dolly Varden trout and at least one of the 4 endemic species of *Cottus,* namely *C. tenuis,* definitely appear to be Ice-Age relicts, and call for a passable outlet during one of the Glacial periods. Their ancestors presumably ascended the Klamath system before Klamath Falls were formed or when the falls were flooded over.

The long isolation and long lake history of the Klamath basin are vouched for by the lacustrine modifications and by the high endemism exihibited by the fish fauna. Adaptations for life in lakes are exhibited to a strong degree by the lake suckers and by *Cottus princeps,* and in an incipient way by one of the subspecies of *Siphateles obesus.* Ten of the 25 fish species known from the Klamath system (including anadromous and euryhaline types from the lower river) are endemic, yielding the high ratio of 40 per cent. One of the 25 species is differentiated into 2 endemic subspecies. The one species that is separated generically gives an endemic value of 8 per cent for the 13 genera of the basin. The Klamath fish fauna (Miller, 1946*b*) approaches that of the Columbia, Sacramento and Colorado in richness and distinctness.

As Gilbert (1898) and Snyder (1908*c*) pointed out, the Klamath River fish fauna is sharply differentiated from the Sacramento and Columbia faunae, both of which are represented by derived faunulae in the opposite coastal streams. Thus no *Ptychocheilus* occurs in the Klamath, though the genus is present both to the north and to the south. There are a number of closely related, representative species in the three systems, and some past connections must have existed. The connections were probably headwater ones, because none of the genera distinctive of the Sacramento or of the Columbia occur in the Klamath. It was presumably by headwater captures that the ancestor of *Catostomus rimiculus* was derived from *C. syncheilus* (Hubbs and Schultz, 1932*b*) of the Columbia system, and it was almost certainly by such a connection that *C. rimiculus* moved from the Klamath northward to the Rogue River, or *vice versa*. This is the only strictly fresh-water fish in the Rogue; in the Klamath it occurs only in the streams below the falls.

There are some fish-faunal indications that there may have been a connection between the Klamath River system and the drainage basin of Pit River, now a Sacramento tributary. Thus the subspecies of *Siphateles obesus* in the respective drainages are strikingly similar. A dwarfed, nonparasitic derivative of the Pacific lamprey is known only from these two waters. *Cottus asperrimus* and *Cottus macrops,* of restricted range in Pit waters (Rutter, 1908), are much like *C. tenuis* and *C. klamathensis* of the Klamath (*macrops* and *klamathensis* are particularly close). The Klamath and Pit subspecies of *Rhinichthys osculus* are also much alike, but are not of clear-cut zoogeographic value. The Pit River fishes which seem related to Klamath types appear to be relicts confined to headwaters, particularly to the Fall River system above its falls —as though an original Klamath stream fauna had been nearly overwhelmed by a more aggressive Sacramento fauna that entered the region as the Pit River cut back onto the lava plateau, to capture some of the interior drainage (Keyes, 1918). Pleistocene lake beds in the region, shown on the map by Jenkins (1938), indicate that these events were relatively recent.

There are some similarities between the fish faunas of Goose Lake (at the head of the Pit) and of Klamath Lake (Cope, 1883; Gilbert, 1898; Snyder, 1908*b*). We see no good reason, however, to stress Cope's suggestion of a possible union of Goose and Klamath lakes. We do offer for further consideration, the idea that a stream connection existed in some past time, probably in the Pleistocene, on the "Interior Platform," between Goose Lake and Pit River on the one side and the Klamath basin on the other side. Whether the connection involved the discharge of the Pit into Klamath Lake waters or some form of stream piracy is not obvious. The evidence may well lie buried under the relatively recent, intervening Modoc Lava Flows (Peacock, 1931; Anderson, 1941). In this lava region, however, Anderson noted suggestions of Pluvial lakes other than Medicine Lake, one of the Caldera lakes described below.

CALDERA LAKES

There are a few isolated lakes in the west that occupy the basins of calderas, depressions produced by the explosive disruption of volcanic cones. These lakes are naturally without native fish life. The best example is Crater Lake, Oregon. Another is Medicine Lake, California.

41*b*.—**Crater Lake**

This famous lake occupies a large caldera on the divide between the Klamath system and the coastal drainage to the westward. It is totally devoid of native fish life, but introduced trout have become established (Evermann and Meek, 1898; Kemmerer, Bovard and Boorman, 1923; Hasler, 1938; Hasler and Farner, 1942). The lack of fishes is quite in line with the assumed cataclysmic origin of the lake (Atwood, 1935; Williams, 1942), and suggests that the lake has never overflowed its high rim. However, at least one of the mountain lakes in the Klamath drainage, namely Lake of the Woods, also seems devoid of native fishes.

41*c*.—**Medicine Lake**

In the basin of a collapsed caldera on the generally dry Modoc Lava bed, in northern California, south of the "Oregon lakes," there is a rather deep body of water, Medicine Lake, which was larger in Pluvial times (Peacock, 1931; Anderson, 1941). The two subspecies of fish at hand from this basin, *Rhinichthys osculus* and *Siphateles obesus,* seem indistinguishable from the Pit River representatives, but the material is inadequate to clinch this point. It is highly probable that these fishes were introduced from Pit River, just to the southward. Anderson (personal communication) indicates that on geological grounds it is almost certain that Medicine Lake never discharged. Joseph H. Wales of the California Division of Fish and Game writes that this lake is a favored fishing spot, that it has long been stocked with game fish, and that fishermen bring in live minnows. We have not visited the Medicine Lake basin.

A considerable number of small basins on the "Interior Platform" of northeastern California contain or once contained isolated lakes. These occur not only on the Modoc Lava Flows but also in other areas where the topography has been modified by relatively recent lava flows, for instance to the east of Lassen Peak (Williams, 1932). These lakes seem to have received little attention from physiographers and none from ichthyologists.

DISRUPTED PARTS OF SACRAMENTO RIVER SYSTEM

The Central or Great Valley of California drains through the Sacramento and San Joaquin rivers into San Francisco Bay, but some of the headwaters have become partly separated.

42.—**Goose Lake**

Various authorities (Russell, 1884; Snyder, 1908*b–c*; Rutter, 1908; Van Winkle, 1914, and others) have commented on the Goose Lake basin as one which has shifted back and forth between the areas of interior and exterior drainage. Its occasional Recent overflows into the Pit (a Sacramento tributary) place it faunistically as a part of the Sacramento system, and this relationship is not lost when, as a result of lowered lake levels, Goose Lake ceases to discharge into Pit River, and becomes by this technicality a part of the interior drainage of the Great Basin. The native fish fauna of Goose Lake (map 1, no. 42), typically that of the upper Sacramento, includes the Pacific lamprey, *Entosphenus tridentatus,* apparently in the form of a semi-degenerate race (Hubbs, 1925); a cutthroat trout (presumably now extinct); the Sacramento sucker, *Catostomus occidentalis,* of which the local form has been described as a subspecies (Fowler, 1913); an endemic subspecies, *thalas-*

sinus (apparently now extinct), of the widespread chub, *Siphateles obesus*; a dace, *Rhinichthys osculus*, apparently inseparable from the Pit River form; another minnow, *Hesperoleucus symmetricus mitrulus* (Snyder, 1913), of a typically Sacramento genus and upper Sacramento subspecies; and a *Cottus*, of the coastwise *gulosus* type.

42*a*.—**Clear Lake**

About 100 miles north of San Francisco lies the basin containing Clear Lake, the drainage of which may be considered a disrupted part of the Sacramento system. The outlet, Cache Creek, normally sinks long before reaching the Sacramento River. The late geological history of the drainage of Clear Lake, as determined by Davis (1933), was rather complicated. The plain now occupied by this lake formerly drained both to the northwest, into the Russian River, a coastal stream, and to the eastward, into the Sacramento. A small lava flow later disrupted the upper segment of the eastern stream, thereby diverting its waters (and its fish fauna) into the western stream, and consequently into the Russian River. Still later a great landslide blocked the western outlet, thereby forming the predecessor of the present Clear Lake, which subsequently rose and cut through the lava dam to the east to establish the present drainage relations. Holway (1907) had apparently misinterpreted this physiographic change. This drainage history provides an explanation for the occurrence of certain Sacramento species, as noted by Snyder (1908*a*), in the Russian River. That the Clear Lake basin contains a Sacramento fish fauna has been conclusively shown by Jordan and Gilbert (1894), Smith (1896), Coleman (1930), Lindquist, Dionier and Hancey (1943), and Murphy (1944).

42*b*.—**Lake Tulare**

Except in extremely humid periods about one-third of the central or Great Valley of California is, like the Goose Lake basin, a region of interior drainage. The barrier is not one of lava, as it is at Goose Lake, but consists of alluvial fans. This semi-isolated drainage area is known to physiographers as the Tulare Basin, though it is more or less completely divided by the alluvial fan of Kern River into two main basins, that of Tulare Lake, fed by Kings, Kaweah and Tule rivers, and that of Buena Vista Lake, receiving Kern River. Smaller marshy lakes intervened a century ago (Blake, 1857). These divisions have been connected in historic periods of high water, and at such times the surface waters of the upper San Joaquin Valley have discharged through Fresno Slough (Tulare Lake Slough) into the San Joaquin River (Blake, 1857; Mendenhall, Dole and Stabler, 1916; Holmes, Eckman, Nelson and Guernsey, 1921). An early explorer wrote of this large lake in San Joaquin Valley as becoming smaller. An ancient lake in the Tulare Lake basin has been described briefly by Arnold and Anderson (1910). This lake was first thought to be of late Pleistocene age, but more recently the opinion has been expressed that its two stages (known only from clay deposits) are earlier Pleistocene (Barbat and Galloway, 1934; Flint, 1947). Almost certainly there was, however, a considerable expense of water, at least in the southern part of the San Joaquin Valley, during the Pluvial period. A line of dunes bordering smooth flats near the south end of the basin floor seems to have been formed by a large body of water, now represented by Buena Vista Lake, that was probably part of a large Pluvial Lake Tulare. It has even been suggested that the whole lower part of the Central Valley was occupied in relatively recent times by an immense lake. Blake (1857) found shells of fresh-water mollusks widely scattered over the surface of the valley and in text and by map indicated his belief that such a lake existed. We were at first disposed to accept this view and Pluvial Lake Tulare (no. 1) was shown as very large and of unindicated northward extent on the map presented by Miller (1946*a*). Now, however, we disfavor this interpretation and suspect that the shells seen by Blake were the remains of mollusks that had lived not long previously in shallow temporary pools. Such shells are commonly found on flat coastal plains. There appears to be no shore-line or other evidence of a lake so large and so deep (300 feet). It is improbable that there was enough precipitation to produce such a lake at any relatively recent time other than the Pluvial when the lowered sea-level presumably lay far below the Strait of Carquinez, the only place where the necessary block could likely have existed.

The Tulare basin contains the Sacramento fish fauna, including the several endemic genera of that system (Miller, 1946*b*). *Siphateles obesus formosus,* a lacustrine type, was obtained here in early years, but has not been seen here or elsewhere in recent times. Local endemics described from the mountain part of the Kern River are trouts: *Salmo gilberti, S. rosei, S. agua-bonita, S. whitei* and *S. roosevelti.* Some of these nominal species, however, do not appear to be valid. An examination of the types of *S. rosei* and *S. gilberti* shows them to be inseparable and this local form seems to be only a subspecies (*S. gairdnerii gilberti*). *S. rosei* appears to represent an introduction. *S. whitei* and *S. roosevelti,* described by Evermann (1906) as very local forms of the golden trout, seem at most to be subspecies of *S. agua-bonita.* Their validity, even as subspecies, particularly that of *S. roosevelti,* has been questioned (Curtis, 1935*a*–*b*). A local form of sucker (*Catostomus*) may also be endemic.

In the rain-shadow of the Coast Range, the western tributaries of the Tulare portion of the Central Valley have become reduced to dry washes or disconnected hill streams. Only two of these streams have been thoroughly examined for fish life, namely Los Gatos and Waltham creeks. These creeks, which cease to flow near Coalinga (Arnold and Anderson, 1910), have a puzzling fish fauna. The three species seem inseparable from those of the Monterey Bay streams (the fauna of which, as previously noted, was derived from that of the Sacramento system, but at so remote a time that considerable differentiation of the fishes has ensued). No topographic reason for this fish relationship is now apparent. Recent transfer by man is a possible as well as a plausible explanation.

42*c*.—MINOR COASTAL STREAM SYSTEMS

Various coastal streams north and south of Golden Gate may also be regarded as disrupted parts of the Sacramento and Columbia systems. The correlated geological and ichthyological data have been treated by Snyder (1905, 1908*a, c,* 1913, 1916), and by Branner (1907), Holway (1914) and Davis (1933).

42*d*.—Lake Carrizo

A basin in the Coast Range of California, containing salt lakes and traces of a Pluvial lake, may be treated as a disjoined portion of the system of Salinas River (one of the Monterey Bay streams). This basin is known as Carrizo Plain and the salt lake as Soda Lake (Arnold and Johnson, 1909; Gale, 1913*d*; Free, 1914*a*). It is highly probable that this lake was at least semipermanent in Pluvial times, but no evidence was found (in May, 1947) to indicate that it rose high enough to discharge into San Juan Creek of the

Salinas system or that it contains fish. At a time not very remote, however, it probably contained more water, for Indian paintings, on Painted Rock, and other artifacts indicate the human occupation of this now very dry basin. We suggest that the ancient lake be known as *Pluvial Lake Carrizo.*

DISRUPTED PARTS OF COLUMBIA RIVER SYSTEM

Within the Columbia River system, on the arid lava expanse of the Columbia Plateau, there are numerous basins that may be regarded as of interior drainage, at least in so far as the surface water connections of the present time are concerned. The more important of these basins are discussed briefly.

42*e*.—**Fort Rock Lake**

Following the findings of Cope (1883, 1889), Russell (1884), Snyder (1908*b*) and Waring (1908), the Pluvial lake in this Oregon basin has generally been treated as one of the interior-drainage lakes, but according to Allison (1940, 1946) it discharged into the Columbia River system. Van Winkle (1914) had suggested that it probably had an outlet. Fort Rock Lake (to use the name proposed by Allison, 1940) centered near the intersection of the parallel of 43° 15′ and the meridian of 120° 45′. Its bed includes the subsidiary basins of Silver Lake and Paulina Marsh, and of Thorn Lake, Fossil Lake and Christmas Lake, as well as a considerable expanse of flat desert about Fort Rock to the northwest (Figs. 17–19). The compound basin seems to be wholly enclosed, but according to Allison's preliminary report (1940) and verbal communication, an outlet lies buried beneath more than 100 feet of postlacustrine lava flows. Beyond the lava the abandoned outlet river channel extends via Long Prairie to Deschutes River, a Columbia River tributary. A discharge in this direction had already been postulated by Free (1914*a*), but without adequate supporting evidence.

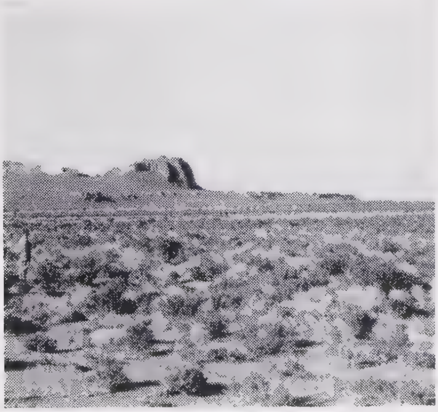

Fig. 17. Terraces of Fort Rock Lake, north of Silver Lake.

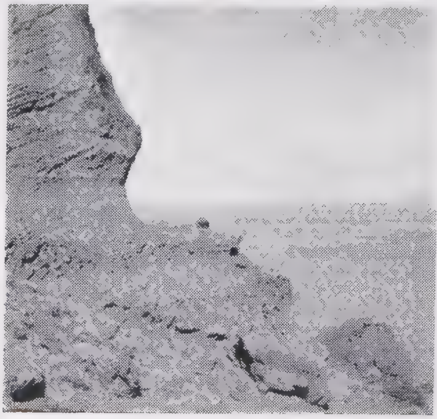

Fig. 18. Wave-cut notch in Fort Rock. Photographs by Ira S. Allison

The Recent fish fauna of the Fort Rock Basin (Cope, 1883; Snyder, 1908*b*, and personal observations) does not provide conclusive indications as to the drainage relations. This fauna could have been derived from the Columbia River system, from the Klamath, from the upper Sacramento, or from one of

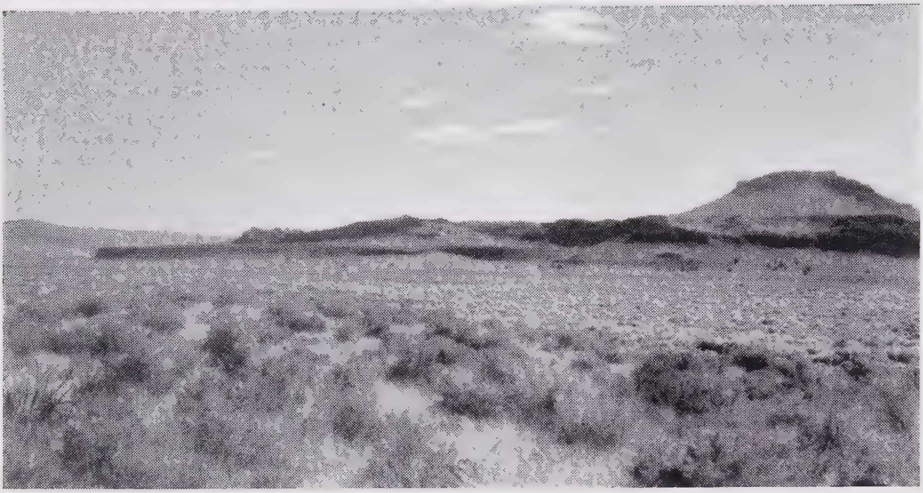

Fig. 19 Terraces of Pluvial Fort Rock Lake, Oregon. Photograph contributed by by Ira S. Allison.

the Oregon lakes of interior Pluvial drainage. The known Recent fishes of the basin are cutthroat trout, probably now wholly supplanted by introduced rainbows; a dace, *Rhinichthys osculus,* of little zoogeographic significance; and a chub, belonging to the species *Siphateles obesus,* which is common to nearly all of the drainage systems of the general region. However, the characters of this form appear to agree more closely with those of the Klamath representative (*S. o. bicolor*) than with those of any of the other populations in the neighboring drainages. Perhaps this chub gained access to the Fort Rock basin by a stream capture or stream transfer in the vicinity of Sycan Marsh (in the upper part of Sycan River, in the Klamath basin), across the low divide that here separates the Silver Lake and Klamath drainages.

The Pluvial fish fauna of Fort Rock Lake, as represented by fossil or semi-fossil remains from the bed of Fossil Lake, is more illuminating. Cope (1883, 1889) described from these deposits two suckers (Catostomidae) and three minnows (Cyprinidae), all supposedly different from the Recent fishes of Silver Lake. Shufeldt (1913) illustrated numerous fish bones from Fossil Lake, but did not identify them; furthermore, he erroneously summarized Cope's findings. Jordan (1907) and Allison (1940) reported that jaws of large salmon are abundant in the Fossil Lake beds, and this was one of the reasons behind Hay's doubts (1927) that the lake was enclosed and behind Allison's belief that Fort Rock Lake had a Pluvial connection with the ocean. The two Fossil Lake species of suckers referred by Cope to *Catostomus* were reservedly placed by Starks (in Jordan, 1907) in *Chasmistes.* If this reference should prove to be correct, Fossil Lake would appear to have a faunal relationship with the Klamath Lakes, Lake Lahontan and Lake Bonneville, as well as with the Columbia River. A provisional examination of newly collected fish remains from Fossil Lake, obligingly made available to us by Prof. Allison, indicates that they are referable to at least two species of large suckers, probably *Chasmistes;* salmonids, in part at least *Oncorhynchus;* and a minnow. The rich fossil bird fauna of the same lake bed is treated as Pleistocene (Shufeldt, 1891, 1892, 1913; Miller, 1911; Howard, 1946). The inclusion of a flamingo (on reliable evidence, we are assured by Dr. Loye Holmes Miller and Dr. Hildegard Howard) does not necessarily indicate a warm climate, for in South America flamingoes range far into the Temperate Zone. Among the mammals of the Fossil Lake beds (Hay, 1927: 243–244) there are included both ordinary beaver (*Castor*) and the giant beaver (*Castoroides*), the occurrence of which indicates that the country surrounding Fort Rock Lake must have been wooded land, rather than the desert (Figs. 17–19) that now characterizes the dry bed of the ancient lake. The ages of two layers of fossils in Fossil Lake were discussed by Hodge (1930).

42*f*.—**Lake Malheur**

Also known as Harney basin, the Malheur basin, on the plateau of southeastern Oregon, is generally included in the Great Basin, although it is clearly a disrupted fragment of the Columbia River system. Russell (1884) first stated that the Pluvial lake of this basin (for which the name *Lake Malheur* seems appropriate) had an outlet, but later he (1903*a*) and Waring (1909) indicated that this shallow lake was formed by a lava block, in Malheur Gap, across the former stream course by which Silvies River discharged through Malheur River into Snake River and thence into the Columbia. From the physiographic evidence these authors concluded that Lake Malheur never rose to the level of the top of this lava dam. Even with the more precise levelling now available, Piper, Robinson and Park (1939) were uncertain as to the discharge. Some physiographic features suggest an overflow, but the crest of Malheur Gap stands about 9 feet above the top of the highest beach ridge. Perhaps the lake rose, as did Pluvial Lake Madeline (p. 58), until seepage through the fissures of the lava balanced the inflow.

Snyder (1908*b*) showed conclusively that the fish fauna of the Malheur basin confirms this hydrographic history: "The first haul of the seine-net in Silvies River, which brought out such forms as *Acrocheilus alutaceus* and *Ptychocheilus oregonensis,* indicated plainly that it also bears a close faunological relation" with the Columbia system. Snyder failed to find evidence "that the fishes which are isolated in the Malheur basin have visibly differentiated from their congeners in the Columbia." We, however, are able to detect enough distinctions to recognize 4 or 5 endemic subspecies in this isolated system. This moderate degree of speciation suggests a somewhat prolonged isolation, perhaps from late Pleistocene time. The total fish fauna of the Malheur Basin seems to comprise 4 families, 8 genera, 10 species, and a total of 12 forms including subspecies.

Van Winkle (1914) thought, and then doubted, that Lake Warner discharged into Lake Malheur. There is nothing in the ichthyological evidence to disprove this idea, though if such a connection existed, one would expect to find a different and a richer fauna in the Warner waters.

42*g*–*n*.—**Other Waters**

A multitude of other creeks and lakes that were formerly tributary to the Columbia River have been set apart by various physiographic processes. Those that seem most significant in connection with Great Basin problems are discussed briefly.

42*g*.—COW LAKE.—As Russell (1903*a*) pointed out, Cow Lake lies in a basin that was cut off by a seemingly recent lava flow from the Owyhee River of the Snake drainage in eastern Oregon. So far as we can see the fish fauna of the tributary Cow Creek is still undifferentiated from that of the Columbia River system.

42*h–j*.—CRAB CREEK BASIN AND OTHER WATERS ON CHANNELLED SCABLAND.—Crab creek (Russell, 1893; Calkins, 1905; Schwennesen and Meinzer, 1918) is a disrupted tributary (no. 42*h*) of the Columbia in eastern Washington. The upper part contains a number of undifferentiated Columbia River types, including *Catostomus syncheilus* Hubbs and Schultz (1932*b*). Formerly, at least, it also contained a cutthroat trout, which Evermann and Nichols (1909) described as an endemic species, but which we would treat as a subspecies (*Salmo clarkii eremogenes*). This part of the creek occasionally flows into Moses Lake (no. 42*i*) in Grand Coulee. The U. S. Geological Survey state base map erroneously shows Crab Creek as a tributary first to Soap Lake, a highly saline lake in Grand Coulee, north of Moses Lake. These are but two of numerous more or less isolated lakes (no. 42*j*) on the "Channelled Scablands" of eastern Washington (Russell, 1893; Bretz, 1923, etc.; Flint, 1938). Except for Moses Lake, none of these waters have been explored by ichthyologists. Moses Lake, containing an isolated endemic subspecies of *Siphateles obesus* (a species mostly confined to the Great Basin), had no surface outlet, for it is blocked by the sand dunes by which it was formed (Calkins, 1905; Schwennesen and Meinzer, 1918). Seepage from the lake forms the lower Crab Creek, which still flows into the Columbia. A race of *Siphateles obesus* distinct from that of Moses Lake, and less modified for lacustrine life, occurs in the lower creek.

42*k–n*.—ISOLATED STREAMS OF THE SNAKE RIVER LAVA PLAIN.—North of the Snake River, Idaho, is a large area where streams from the mountains feed into Mud Lake or into usually dry sinks to the westward. Physiographers have not regarded this area of the Snake River Lava Plain as one of interior drainage, because the waters percolate through the Pleistocene lava to emerge as large springs along Snake River. From a zoological standpoint, however, the drainage is to be treated as interior—at least isolated—for the underground flow can have little if any effect on the distribution of fishes and other animals. The geology and hydrography of the region has been described in detail by Russell (1902) and by Stearns, Crandall and Steward (1938). The fish fauna of the Mud Lake–Lost River group of streams (42*k*) has not been published on, but we have explored the area. In the several streams (Camas, Medicine Lodge and Birch creeks, and Little Lost and Lost rivers) we found 3 species: an endemic subspecies of cutthroat trout; the Dolly Varden trout (probably a Glacial relict, rather than an introduced fish); and 5 highly localized, endemic subspecies or races in the genus *Cottus*. None of these species are Bonneville types, despite the fact that the stream complex lies in the upper part of the Snake River system, which in general has a Bonneville fauna. As mentioned on page 31 these fishes seem to be relicts of the old Snake River fauna, as it existed prior to the time of the destructive lava flows and of the Lake Bonneville discharge. Some Bonneville species do occur in Mud Lake, but definite evidence was obtained to indicate that they were introduced by a bait fisherman.

The Wood River group of streams, just west of Lost River and the Craters of the Moon lava beds in Idaho, exhibits partial isolation and disruption, coupled with faunal peculiarities. According to earlier maps and local usage the Wood River system comprises Big Wood River and Little Wood River, which unite to form Malade River, but the U. S. Board on Geographic Names has ruled that the lower, permanent part of the stream, in Malad (not Malade) Canyon, shall be known as Big Wood River. Starting from the east the first element of this group is Lava Lake (42*l*), with one small tributary from the north. This lake was probably at one time tributary to the Wood River system through Fish Creek, but it is now definitely cut off. In the dry year of 1934 the bed of Lava Lake was dry and the inlet, wholly consumed in irrigation, apparently contained no fish. Fish Creek (42*m*) ends in a marshy sump separated from Little Wood River by a slight alluvial rise. Since the water was first used for irrigation there is said to have been no connection between Fish Creek and Little Wood River, and local testimony is in disagreement as to a former linkage. That such a connection once existed is unequivocally shown by the ichthyological data, for Fish Creek contains a Wood River fauna, including *Cottus leiopomus*. The Wood rivers (42*n*) proper contain a fish fauna that is in part very peculiar. *Salmo clarkii, Catostomus syncheilus* (local subspecies?), *Rhinichthys osculus* and *R. cataractae* probably represent the old Upper Snake fauna (prior to the lava flows). The two other species are noteworthy. One is a local form of *Snyderichthys copei,* a Bonneville species that also is known, very locally, from the Upper Snake (Simon, 1942, as *Gila copei*). The occurrence of this Bonneville species below the main falls, in an area occupied by the true Columbia River fauna, is somewhat anomalous. Its introduction through the Twin Falls Northside Canal might be offered as an explanation, were it not for the fact that the species was recorded from Little Wood River in 1894, whereas the canal was not completed until 1907 (Youngs, Trail and Young, 1933). The Wood River race has probably been isolated for a long time, for it shows some distinctive features (Miller, 1945*a*). The other notable species is a well-marked endemic, *Cottus leiopomus*. The distinctiveness of this sculpin is related to the isolation of the Wood River fauna. The rush of water in the lower river, in Malad Canyon (due to huge springs discharging water from the Snake River Lava Plain) forms rapids and falls that are impassable for most fish, and above this flow the system for a considerable distance is dry except in flood. The physiographic relations involved have been treated by Russell (1902) and by Stearns, Crandall and Stewart (1938); the ichthyological data, by Gilbert and Evermann (1894). We have also studied the area and the fish fauna.

There are several other disrupted portions of the Columbia River system, but they have not been explored ichthyologically. Hubbs and Schultz (1932*a*) thought that *Cottus tubulatus* is confined to the generally disconnected upper waters of the North Fork of Clearwater River in Idaho, but we have since determined that the same or a very similar type occurs in other headwater streams in the Columbia River system.

DEATH VALLEY SYSTEM

Ranking third in area and in faunal diversity among the interior drainage basins is the Pleistocene Death Valley System, now greatly disrupted and occupying several isolated valleys and basins in the desert region of eastern California and adjoining parts of Nevada (Miller, 1943*a*, 1946*a*, in press). The late physiographic history of the rivers and lakes in this area is divisible into at least two stages, which have been correlated tentatively by Blackwelder (1931: 918) with the Tahoe and Tioga stages of glaciation in the nearby Sierra Nevada Range. These stages, in turn, are believed to have been approximately contemporaneous with the earliest and latest stages of the Wisconsin or last continental glaciation in eastern North America (Blackwelder, 1933: 464–471; 1936: 311). Still earlier phases are also probably represented. Lake Manly (map 1, no. 50), the last large Pleistocene lake in Death Valley, was the sump for the waters of this system, which drained from the Mohave Desert, Amargosa Desert, and Owens Valley (via the Indian Wells, Searles, and Panamint basins—map 1, nos. 48, 49). In addition, Lake Pahrump (Miller, 1946*a*; map 1, no. 52), which lay along the California–Nevada line east of Death Valley, is believed to have discharged into the Amargosa River, a tributary of Death Valley, during the maximum extent of Pleistocene waters. Similarly, a Pleistocene lake filled Adobe Valley (Miller, 1946*a*; map 1, no. 46), and its waters rose to cut an impressive outlet (Fig. 20) into the now virtually dry North Fork of Owens River. The continuity of the entire hydrographic system, and hence of the fish distribution, very probably antedates the last Pluvial periods (pre-Tahoe glacial stage).

The early maps of Quaternary lakes in the Great Basin by Russell (1885) and Gilbert (1890) showed discrepancies for the lakes of this system. Russell omitted Lake Owens (map 1, no. 47) and charted Lake Searles (no. 48) and Lake Panamint (no. 49) as one body. The lake in Death Valley, now known as Lake Manly (no. 50), was drawn so as to include the lower end of the Mohave River basin (Lake Mohave, no. 53), a view since unsupported by geological facts. The outline of Lake Thompson (no. 57A) was incorrect. These errors were repeated by Gilbert except that he included, in rough outline, Pluvial lake Owens.

Lee, Stone, Gale and others (1915) presented a map (fig. 10, p. 82) which is too inclusive for the Amargosa–Mohave drainage basin and which erroneously included Lake Mono (no. 43) in the hydrographic basin of Lake Lahontan. The same map was reproduced by Boutwell (1933: 12). The lakes of this system were very inaccurately mapped, in respect to outline and position, by Jones (1940).

According to our present estimates, the native fish fauna of this system comprises 3 families, 5 genera, 10 species, and at least 24 kinds in all. There is only one endemic genus, the cyprinodont *Empetrichthys,* perhaps derived from an ancestral form in the Colorado River basin but more likely a very old relict. Its nearest living relative is *Crenichthys,* a genus occurring in the Railroad Valley system (pp. 90–94) and the drainage of Pluvial White River (pp. 96–98). Both *Empetrichthys* and *Crenichthys* were presumably derived from *Fundulus,* perhaps from a species similar to the fossil, *F. curryi,* recently described from Death Valley (Miller, 1945*c*: 315–319, fig. 1). The comparatively high number of total forms in the Death Valley system is correlated with the great disruption which this complex has undergone during and since late Pleistocene time. High endemism on the species level is attributable to the early Wisconsin or pre-Wisconsin origin of the fauna, both from the north and from the south. The Pleistocene hydrography of this drainage has been reviewed and correlated with fish distribution in a recent paper by the junior author (Miller, 1946*a*).

43–44.—**Mono Lake Basin**

The physiography and geology of the Mono basin, lying along the California–Nevada boundary line south of Lake Lahontan, was treated in masterful style by Russell (1889). He did not believe that Pluvial Lake Mono (map 1, no. 43) had an outlet. Whitney (1865: 452) and Russell himself (1883: 204) had earlier indicated, with doubt, and erroneously, that Lake Mono was tributary to Lake Lahontan. As Russell suggested there may have been a Prepluvial discharge northwestward through Aurora Valley, Nevada, into a tributary of the East Walker River of the Lahontan drainage, but this outlet, if it existed, would have been blocked by lava flows, in part Postpluvial but in part probably Prepluvial. A Pluvial outflow through this channel was disallowed by Russell when he found by levelling that the highest shoreline of Lake Mono is about 100 feet lower than a divide across Aurora Valley.

Between this divide, which lies close to the position of 38° 15′ N. Lat., 118° 45′ W. Long., and the lava barrier discussed above, lies a basin about 2 miles long, in which Russell (1889) found evidence, in the form of faint beach lines, of a small body of water, for which we propose the name *Pluvial Lake Aurora* (map 1, no. 44). It was about 1 mile long and 40 to 50 feet deep, but its basin is now dry. It apparently did not rise high enough to drain into Lake Mono, though a precursor may have discharged either that way or, prior to the lava blockade, into Walker River. Without supporting evidence Free (1914*a*: 39, pl. 1) regarded the independence of the smaller basin as "post-Lahontan" only. Flint (1947: 471) misplaced Lake Aurora in the basin of Whisky [Flat], which lies across a mountain range in the Lahontan system.

It is also highly probable that a waterway once connected Lake Mono with the headwaters of Owens River, just to the south. As is well known, the Mono Craters, which form a chain directly south of Mono Lake, are of recent origin and Putnam (1938, 1940) indicated that these craters erupted after the formation of the Tioga glacial moraines. In 1947 he found (personal communication) clear evidences of an outlet from Lake Mono into the Owens River basin. The course was through now depressed troughs into and through Adobe Valley. In disagreement with Russell (1889), he found the intervening divide to correspond precisely in elevation with the Tahoe, but not the Tioga, level of Lake Mono. This discharge would have allowed fish to move southward from the Mono basin into the Owens system and beyond, but not in the opposite direction for the outlet of the Adobe basin was too steep (p. 80).

The presence of the minnow *Siphateles* in the Death Valley system is highly significant in interpreting the past hydrography of this region. *Siphateles* is unknown from the entire Colorado River fauna, either as a Recent or as a fossil member, but is abundantly represented in the Lahontan basin and other systems to the north and west (Snyder, 1908*b*: 78, 86–97; 1917*a*: 60–67). Its presence in Owens Valley and Mohave River calls for a former connection between the Lahontan and Death Valley systems, and the most plausible route for such a connection is through the Mono basin. Assuming that the transfer of *Siphateles* (as well as of *Catostomus* and *Rhinichthys*) was thus effected, there is now no evidence of remnant populations of these genera in the Mono basin, although several introduced species have become well established there (Vestal, 1942, 1943; Smith and Needham, 1942). We assume that the great and relatively recent deluge of volcanic ash destroyed the fish fauna of the Mono and Adobe basins. Such an hypothesis could explain the present absence of native fishes in these basins and is similar to the hypothesis we advance (pp. 30 and 76) to explain the destruction of fish and other life on the Snake River lava plateau.

45–47.—**Owens River System**

Owens River is the largest of the three major, permanent streams in the Death Valley system. It rises in snow-fed lakes 9,000 to 10,000 feet high along the eastern escarpment of the Sierra Nevada Range, and receives many clear tributaries during the 130-mile course south to its sump, Owens Lake. During Pluvial time its basin contained three sizeable lakes, the lowermost of which, Lake Owens, overflowed to the south and east, to form a chain of lakes by which Owens River discharged for a time into Death Valley (map 1, nos. 45–50).

45.—Long Valley Lake.—Long Valley, the northwestern extension of Owens Valley in southern Mono County, California, lies in the headwater area of Owens River, about 6,900 feet above sea-level. The river makes an abrupt descent through a lava rim from this valley to Owens Valley, dropping 2,400 feet in about 20 miles. Long Valley was the site of a large Pluvial lake (map 1, no. 45) which was briefly described and named Long Valley Lake by Mayo (1934). Its existence had been noted earlier by Lee (1906: 15–16) and its deposits were roughly mapped by Spurr (1903, pl. 1). Later it was mapped by Jenkins (1938) and by Miller (1946*a*, fig. 1, no. 4); also, with number omitted in 1947, by Flint (1945, 1947).

The evidence of a former lake is demonstrated by the lacustrine deposits on the floor of the valley, by obvious wave-cut terraces, and by tufa deposits which mark the final stages of lacustral history. Some of the terraces cut across glacial moraines which were formed during the Tahoe glacial stage. The lake disappeared when headward erosion by Owens River through the volcanic rim to the east lowered the outlet of Long Valley. Long Valley Lake appears to have been of rather short duration.

The native fish fauna of the Long Valley basin (*Catostomus, Siphateles,* and *Rhinichthys*) is definitely of the Owens River type, but has not been studied in sufficient detail to determine if any local differentiation has taken place.

46.—Adobe Lake.—A long, but rather narrow and shallow, Pluvial lake (map 1, no. 46) once filled a large portion of Adobe Valley, about 35 miles north-northwest of Bishop, in Mono County, California. Its present remnants are Adobe Lake, River Springs Lakes, and Black Lake. At maximum height, the Pluvial lake discharged through a precipitous canyon to cut an impressive outlet gorge (Fig. 20) into the now almost completely dry North Fork of Owens River. The lower end of the lake bed is now occupied by alkaline Black Lake, from which flood waters still discharge through the old outlet gap. This outlet, which according to Gilbert (1941) was formed along a fault

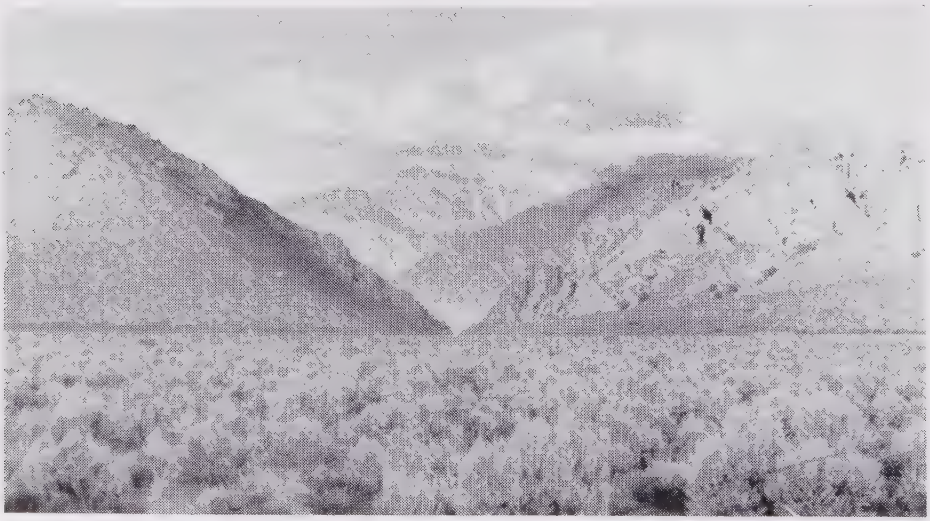

Fig. 20. Outlet canyon of Pluvial Adobe Lake, California, looking eastward toward lofty Boundary Peak of White Mountains. The outlet was too steep for the ingress of fish.

line, is far too steep ever to have allowed the ascent of fish. Thus we account in part for the absence of fish life from the fine springs and creeks of Adobe Valley. Since Adobe Valley lay in the course of the Tahoe-stage outlet of Lake Mono, it presumably once contained fish life, which has since been exterminated by volcanic ash (p. 79). Free (1914*a*: 40) recognized that Adobe Valley was once tributary to Owens Valley and the Pluvial lake was recently mapped and named by Miller (1946*a*, fig. 1, no. 5).

47.—LAKE OWENS.—As long ago as 1865, Whitney recognized that Owens Lake, now landlocked and forming the sump of Owens River, was once a larger body of water which discharged to the south. Several geologists have examined and reported briefly on Pluvial Lake Owens, but it remained for Gale (1914) to describe and map the ancient lake in detail. The following description is condensed from his account. At its maximum height, Lake Owens had an area of about 240 square miles, in contrast to less than 100 square miles for the Recent body (as measured in February, 1913). Evidence for the existence of the Pluvial lake is recorded by elevated beach lines, wave-cut terraces, and sand bars, and also by the obvious outlet channel during the existence of which the lake level was lowered 30 feet. During the period of overflow, and probably for some time afterward, fishes inhabited the lake (as they now do the lower part of Owens River), but its waters are far too briny at present to support fish life.

48–49.—**Owens River – Death Valley Connectives**

Although the Recent drainage of Owens River terminates in Owens Lake, Owens Valley was connected to Death Valley by a continuous waterway during late Pleistocene time. Lake Owens overflowed to form a chain of lakes to the south and east, which occupied, in successive order, Indian Wells Valley, Salt Wells Valley, the Searles basin, and Panamint Valley, from which the waters discharged into Death Valley.

48.—INDIAN WELLS–SEARLES BASIN.—Overflow from Owens River into Indian Wells and Salt Wells valleys and the Searles basin formed, at maximum expansion (map 1, no. 48) a body of water which submerged all three basins and had an area of about 385 square miles (Gale, 1914: 270). According to Blackwelder (1933, 1941), this stage of Lake Searles is probably to be correlated with the Tahoe glacial stage. The depth of water in the Searles basin at that time was approximately 640 feet above the level of the present salt plain, and at this elevation an outlet channel was cut by which the waters of Lake Searles discharged into Panamint Valley, as described below. This overflow ceased after Tahoe time and during the succeeding Tioga glacial stage the waters of Lake Searles had subsided to form two bodies, Lake China (map 1, no. 48A) in Indian Wells Valley and Lake Searles (map 1, no. 48B) in Searles Valley, connected by a stream through Salt Wells Valley.

49.—LAKE PANAMINT.—During its maximum expansion, in Tahoe time, Lake Searles overflowed to fill Panamint Valley, forming Lake Panamint (map 1, no. 49), a narrow body of water 60 miles long and over 900 feet deep. At its greatest height, Lake Panamint is believed to have discharged near its southern end through Wingate Pass into Death Valley, the terminal lake of the series. During this stage the lake had an area of nearly 273 square miles. The greater antiquity accorded this lake is further suggested by the indistinct, though definite, traces of its former levels (Gale, 1914: 312–317). Free

(1914*a*: 41) concluded that if a lake existed in Panamint Valley it was of very short duration and small size and that its highest level lay far below any possible outlet gap.

Neither the Indian Wells–Searles basins nor Panamint Valley contains fish life. The reason is apparent in the first-named basins, for there are either no waters remaining or those that do exist are mountain springs too small to support fishes. Although Panamint Valley contains some fine springs and creeks, it too is fishless—perhaps because mountain springs and creeks in the desert are subject to severe washouts.

50.—**Lake Manly, Death Valley**

The existence of a Pleistocene lake in Death Valley was recognized before the turn of the century by Russell (1885, 1889) and Gilbert (1890). As already explained (p. 78) these geologists mapped the ancient Lake Manly (map 1, no. 50), so as to include also the lower end of the Mohave River basin. This procedure was likewise followed by Bailey (1902), who named the body "Death Valley Lake." It remained for Blackwelder (1933) to accurately describe and map Lake Manly and, since Bailey's lake is far too inclusive and presumably was of earlier age, we have adopted the name of Lake Manly. which was proposed by Means (1932).

Lake Manly was fed principally by waters from Owens River, via Lake Searles (higher, Tahoe, stage) and Lake Panamint, and from the conjoined Amargosa and Mohave rivers—all of which entered the lake near its southern end. According to Blackwelder (1933: 470), the lake is probably to be correlated with the Tahoe (or earliest Wisconsin) glacial stage, for its deposits

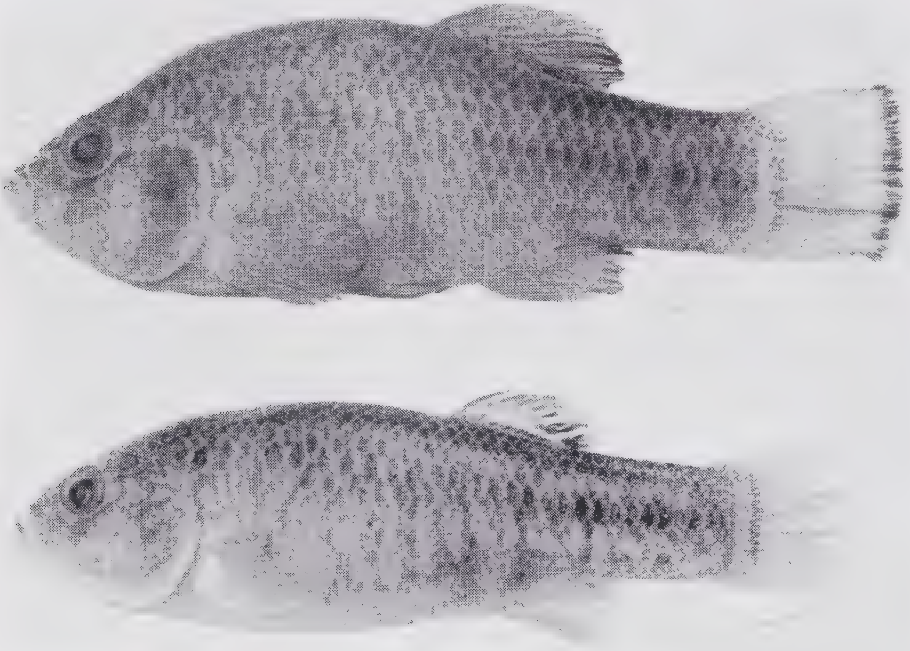

Fig. 21. **Cyprinodon salinus** Miller, a cyprinodont fish restricted to the briny waters of Salt Creek, on the floor of Death Valley. Its specific differentiation dates from the desiccation of Pluvial Lake Manly. Male above, female below.

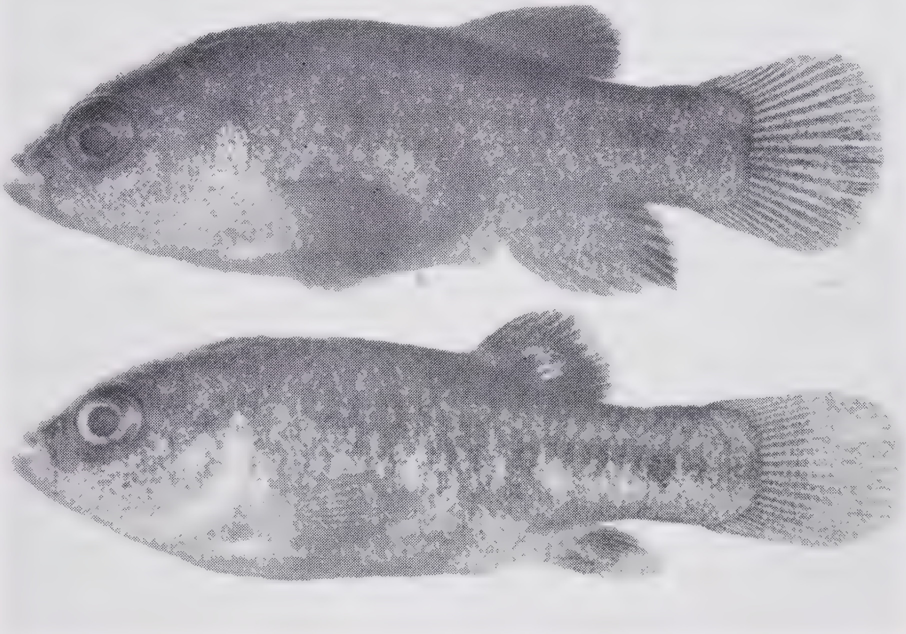

Fig. 22. **Cyprinodon diabolis** Wales, a dwarf cyprinodont known only from a single small spring, Devil's Hole, in Ash Meadows, Nye County, Nevada. Male above, female below.

and terraces, like those of Lake Panamint, have almost been erased by subsequent erosion. At maximum height, Lake Manly was about 90 miles long, 6 to 11 miles wide, and nearly 600 feet deep, and had no outlet. The alternation of salt and clay beds to a considerable depth beneath the present salt plain indicates that Lake Manly was only one, the last, of a series of Death Valley lakes.

The Recent fish fauna of Death Valley is restricted to two species of the saline-tolerant genus *Cyprinodon* (Miller, 1943*a*, 1943*b*, in press). Presumably the *Cyprinodon* which inhabited Lake Manly constituted a single kind and the differentiation of this form therefore dates from the disappearance of the lake and the consequent isolation of the ancestral stock in Salt Creek and in the lower Amargosa River. The evolution of these populations into two very distinctive species is in full harmony with the view that Lake Manly was an ancient body. One of these species, *C. nevadensis,* has evolved into a number of distinct subspecies; the other, *C. salinus* (Fig. 21), is confined to Salt Creek, along with a very distinct mollusk of marine affinities recently named by Berry (1947).

Fossil cyprinodonts described from old lake beds in Death Valley (Miller, 1945*c*) help in the reconstruction of the past fish fauna and hydrography of the region. They appear to represent a species of *Cyprinodon,* a genus still common in this system and that of the lower Colorado, and *Fundulus,* a genus of temperate, lowland areas also represented by a fossil species in Lake Lahontan beds (see p. 26). A species of *Fundulus* still occurs along the coast of California, and another lives in a few isolated waters in the interior of Lower California. Largely on the basis of fish distribution, Blackwelder (1933) suggested that the Death Valley region may once have been tributary to the Colorado River, and Miller (1946*a*) has presented in more detail the fish evidence for such a connection. The presence of *Cyprinodon* in the Death Valley system almost demands such a connection and the occurrence of a fossil *Cyprinodon* in the area indicates that the connection was a rather ancient one. perhaps late Pliocene or early Pleistocene.

51–52.—**Amargosa River System**

The Amargosa River rises above the old mining town of Beatty, in Nye County, southwestern Nevada, and its wash continues south for about 100 miles where it makes an abrupt about face to terminate some 50 miles to the north in Death Valley. During heavy winter floods, it still discharges onto the great salt flat which marks the remnant of Pluvial Lake Manly, but its surface waters apparently have not reached Bad Water, the final sink of the Amargosa on the floor of Death Valley, within historic time. Although its catchment area is greater than that of the Mohave River basin, next to be described, the Amargosa contains the smallest water supply of the three major streams in the Death Valley system. In the headwater region there is permanent water of good quality, but at the few other perennial flows of this "river," the water is saline. In its middle and lower reaches, the Amargosa has appropriately been described as an artery of salt running through the desert. At intervals, however, the Amargosa receives many large, warm springs, most notably in Ash Meadows, southern Nye County, Nevada.

According to Blackwelder (as cited in Wales, 1930: 61), the various springs and disconnected flows of the Recent Amargosa River were united into an integrated river system in Late Pleistocene time—perhaps even as late as a few centuries ago. The fish evidence supports this view, for the spring and creek populations of cyprinids (*Rhinichthys*) and of all but one *Cyprinodon* show only subspecific differentiation in their now isolated waters. The single exception is *Cyprinodon diabolis* (Fig. 22) of Devil's Hole, Ash Meadows, which may have become isolated in Prepluvial time (Miller, in press).

As pointed out in the discussion of Pluvial Las Vegas River (pp. 101–102), there is physiographic, and also some fish, data to indicate that a stream capture took place between the Amargosa River and Indian Springs Valley over the divide to the east of Ash Meadows (Gilluly, 1929). That valley, in turn, may have had an "earlier pluvial" discharge via Las Vegas River into the Colorado River or its antecedent. Thus it is possible that the dace of Amargosa River, particularly the stock in Ash Meadows, were derived from an ancestral Colorado River stock which was once more widespread in the Las Vegas region.

Two Pleistocene lakes are known in the Amargosa basin but the details of their history have yet to be deciphered. As one of us will point out elsewhere (Miller, in press), there is evidence that a lake (or lakes) once covered the Ash Meadows region east of Death Valley Junction, along the California–Nevada boundary. The great dissection of the lake-bed remnants, their almost complete obliteration, and the amount of tilting which has occurred since their deposition, all suggest that the lake was of considerable antiquity—perhaps Early Pleistocene.

51.—LAKE TECOPA.—Bailey (1902) appears to have been one of the first investigators to recognize the former existence of a lake in the Tecopa–Shoshone area, near the Inyo–San Bernardino county line, California. His map of Pleistocene lakes is so inaccurate, however, that we cannot accept the name of "Resting Springs Lake," which he applied to this body of water—particularly because his lake is much too extensive and was misplaced far to the west of the basin containing Resting Springs. We therefore follow the usage of Blackwelder (1936), who briefly described and formally named Lake Tecopa. He regarded the lake as of middle Pleistocene age, but the dating of this and other Pleistocene lakes in the desert region is difficult and uncertain. According to Noble (1931: 65), Lake Tecopa had an area of at least 100 square miles and a depth of approximately 400 feet. Thompson (1929, pl. 8) was the first investigator to map the lake beds accurately, and the outline of Lake Tecopa shown by Miller (1946*a*, no. 10), and repeated herein (map 1, no. 51), was largely compiled from his chart.

Three distinct subspecies (Miller, in press) of *Cyprinodon* and a local form of the dace *Rhinichthys* inhabit the Tecopa basin, but their differentiation almost surely dates from the recent disruption of Amargosa River and not from the desiccation of Lake Tecopa. Unfortunately, fossil fishes, which might prove valuable in deciphering the age of Lake Tecopa, have not been reported from the old lake beds.

52.—LAKE PAHRUMP.—At some time during the Pleistocene epoch, Pahrump Valley, along the California–Nevada line east of Death Valley, contained a lake which was recently named and mapped (Miller, 1946*a*: 49, fig. 1, no. 11; map 1, no. 52 herein). Free (1914*a*: 44) claimed that Pahrump Valley, and its northern re-entrant, Stewart Valley, as well as Mesquite Valley to the south, all drained into Amargosa River during Lahontan time. Whether Pahrump and Stewart valleys (which together comprised the basin of Lake Pahrump) discharged in Tioga time over the low alluvial saddle to Ash Meadows, of the Amargosa River basin, is not known, but Free's inclusion of Mesquite Valley into the same drainage is erroneous. The divide separating Mesquite and Pahrump valleys is much higher than the outlet pass of Lake Pahrump, at the northern end of Stewart Valley, and the low sand-dune hummocks around Mesquite Valley indicate only a shallow Pluvial lake. That this valley discharged into Pahrump Valley during an "earlier pluvial" stage seems certain, as Free hinted.

A discharge from Lake Pahrump into the Amargosa River at some time during the Pleistocene is evident from both physiographic and ichthyological data. The lake bed remnants, near Pahrump Ranch, are about 50 feet higher than the elevation of the lowest divide between Pahrump Valley and Ash Meadows. Their elevated position is attributable, however, to the known tilting and faulting which have occurred since their deposition, but at the same time the divide north of Stewart Valley has increased in height due to the deposition of alluvium from the adjacent mountains. The presence of a unique genus of cyprinodont fish, *Empetrichthys,* in the Pahrump and Ash Meadows basins, supports the physiographic conclusion that they were once an integrated drainage. This relict, confined to the Death Valley system, is found only in the isolated springs of Ash Meadows and Pahrump Valley. Its differentiation into two distinct species (Miller, in press) suggests that the two basins have been isolated for a long period, perhaps since the close of the Tahoe glacial stage.

53–56.— **Mohave River System**

The Mohave River rises on the northern slopes of the San Bernardino Range of southern California and follows a winding course northward onto the desert for about 120 miles, where it finally sinks into the porous sands.

In the headwater area, above 3,000 feet, its tributaries are generally permanent, but the river becomes intermittent as soon as it debouches onto the Mohave Desert. It is the second largest stream of the Death Valley system and, during Late Pleistocene time, its basin was the site of several sizeable lakes, the lowermost of which overflowed for a time into Death Valley (Lake Manly). Three major Pleistocene lakes are known in the Mohave River basin. Parish (1930) stated that a Pleistocene lake existed south of Victorville and was drained when Mohave River near Victorville cut through the granite barrier known as "The Narrows." It is almost certain that this was an "earlier pluvial" lake as no shore features now remain to indicate its former extent and Thompson's detailed report (1929) of the region made no mention of such a body. W. J. Miller (1944) reported other lake beds, presumably of Quaternary age, near Victorville and elsewhere in the general region. These also were likely of "earlier pluvial" age. On a map adapted from Meinzer, Hay (1927) showed a Pleistocene lake south and somewhat west of Pluvial Lake Manix. It appears to lie in the basin of the present playa of Lucerne Lake, east of Victorville.

53.—Lake Mohave.—The Recent playas of Soda and Silver dry lakes, near the town of Baker on the Mohave Desert, form the present sumps of Mohave River. There is unmistakable evidence, however, that during the latter part of Pleistocene time a continuous body of water, named Lake Mohave by Thompson (1921), covered both of these playas. This ancient lake, which was about 40 feet deep and had an area between 75 and 100 square miles (Thompson, 1929: 563–564), has received considerable attention from both archeologists and geologists, most recently in a symposium by Antevs, Bode, and Campbell and Campbell (1937). The last-named authors correlated Lake Mohave with the latest or Tioga glacial stage. Antevs placed the lake in the last Pluvial period, after the maximum of Tioga glaciation, between 15,000 and 25,000 years ago. The outlet of the lake was described by Bode as having cut through 11 feet of granitic rock, suggesting that Lake Mohave was of moderate duration. The occurrence of archeological sites along the highest shoreline, proves that a primitive people lived around the shores of the lake, but not necessarily during Pluvial times (see p. 24). The only fish life remaining in the now arid basin is a local population of the Mohave River chub (Miller, 1938*b*), *Siphateles mohavensis,* which probably has not been long isolated from other populations of this species inhabiting the main river and hence is not of value in attempting to estimate the antiquity of Lake Mohave. The relation of Lake Mohave to the other two lakes in the lower Mohave River basin is uncertain, as is indicated below.

54.—Little Lake Mohave.—As Mohave River builds up its alluvial fan near the mouth of Afton Canyon, about 15 miles west of Soda Dry Lake, it swings back and forth during floods to discharge alternately into Soda Lake and northward into Cronise Valley, which contains the playas of East and West Cronise dry lakes. During heavy floods these dry lakes are transformed into real though very shallow bodies of water. Such a condition prevailed during Late Pleistocene time when a larger Mohave River swung northward long enough to fill both of the Cronise dry lakes and form Little Lake Mohave (map 1, no. 54), so named by Thompson (1921). This lake was small, short-lived, and probably intermittent, judging from the slight development of its shore features. Aside from fishes which are still occasionally washed into the basin by flood waters of Mohave River (Hubbs and Miller, 1943: 346), no fish life has been found.

55.—Lake Manix.—West of the entrance to Afton Canyon, in the northeastern part of the broad valley east of Daggett, there are conspicuous greenish lake beds which mark the remnants of a large Pleistocene lake. This body of water (map 1, no. 55) was first described and named by Buwalda (1914) and has recently received more detailed examination by Blackwelder and Ellsworth (1936). According to those authors, Lake Manix passed through three distinct lake stages, the first two tentatively correlated with the Tahoe and Tioga glacial stages of the Sierra Nevada, and the third lake correlated with the early Recent or close of the last glacial stage. The first lake probably formed the sink of Mohave River for a considerable time and its disappearance is attributed to desiccation. For this reason it presumably had a fluctuating level, determined by the balance between inflow and evaporation. The second lake, caused by a return of moister climate, eventually rose about 20 feet higher, at which level it overflowed its rim and was rapidly drained. The third lake was much smaller than its predecessors and is believed to have originated from an impounding of the outlet formed by the second lake; the obstruction was high enough to form a body of water 150 feet deep. No traces of such a dam have yet been found and the problem of its origin remains unsettled. As mentioned under the account of Lake Mohave, Campbell and Campbell (1937) correlated the maximum rise (stage 2) of Lake Manix with Lake Mohave. That these two lakes, as well as Little Lake Mohave, were approximately contemporaneous seems certain, but the details of their temporal relations are still to be determined.

Fossil fish remains, not examined by the authors, have been reported from the beds of Lake Manix and identified as *Siphateles mohavensis* (Buwalda, 1914; Blackwelder and Ellsworth, 1936). That this species, or a closely related form, inhabited the Pleistocene lakes of the Mohave basin is to be expected, for the Recent *Siphateles* of Mohave River still retains lacustrine adaptations and hence is maladjusted to its present environment (Hubbs and Miller, 1943).

56.—Small Lakes in Outlet of Lake Mohave.—During the period when Lake Mohave overflowed, Pluvial Mohave River filled successively lower basins to the north prior to its junction with Pluvial Amargosa River. These appear to have been merely shallow, local widenings in the river. The upper and middle basins are now entirely devoid of water but the lower one still contains small salt pools (Thompson, 1929: 605), too briny for fish life.

Contributions to the Recent ichthyology of the Death Valley system have been made by Eigenmann and Eigenmann (1889), Gilbert (1893), Kennedy (1916), Snyder (1917*b*, 1918), Wales (1930), Hubbs (1932, 1941*a*), Miller (1938*a*, 1938*b*, 1943*a*, 1943*b*, 1945*c*, 1946*a*), and Hubbs and Miller (1943). The cyprinodont fishes, which make up the major part of the fauna, are treated in detail by Miller (in press). The geological aspects of the problems involved in the Death Valley system and the Mono basin have been treated by Gilbert (1875*a*), Russell (1889), Bailey (1902), Spurr (1903), Lee (1906), Mendenhall (1909*a*), Gale (1913*a*, 1914), Buwalda (1914), Free (1914*a*, 1916), Darton and others (1915), Huntington (1915), Knopf and Kirk (1918), Waring (1920), Thompson (1921, 1929), Noble (1926, 1931, 1941), Gilluly (1929), Parish (1930), Blackwelder (1931, 1933, 1934, 1936, 1941), Means (1932), Ellsworth (1933), Mayo (1934), Blackwelder and Ellsworth (1936), Antevs (1936, 1937), Mayo, Conant and Chelikowsky (1936), Bode (1937), Campbell and Campbell (1937), Jenkins (1938), Putnam (1938, 1940), Curry

(1939), Gilbert (1941), and Miller (1946*a*). The present surface waters of the system are treated by Chapman (1906), Kocher and Cosby (1926), Thompson (1929), Hardman and Miller (1934), Storie and Trussell (1937), Hubbs and Miller (1943), and Miller (in press).

ENCLOSED FISHLESS BASINS ADJACENT TO DEATH VALLEY SYSTEM

Two groups of enclosed fishless basins are separated by the Death Valley system from the similar "Area of Sterile Basins" (pp. 45–51) to the northward and northeastward. Were it not for the evidence of Pleistocene hydrography just presented, the now fishless depressions of Lake Searles (map 1, no. 48) and Lake Panamint (49), of the Death Valley system, could be included in the Area of Sterile Basins (23), along with the group of enclosed basins that lies just to the southward, and west of the Mohave River.

57A–D.—**Lakes West of the Mohave River**

In the western part of the excessively arid Mohave Desert (Thompson, 1929) there are numerous enclosed drainage basins. These depressions comprise an area that is bounded to the eastward by the channels of Pluvial Owens River and Mohave River of the Death Valley system and to the westward by coastal streams (see map in Miller, 1946*a*). A number of the smaller basins contain playas that were probably occupied by only ephemeral lakes in Pluvial times, for even during that period the southern part of the Great Basin was probably rather arid (Meinzer, 1922). No data have been disclosed to support the claim made by Free (1914*a*: 45) that all the minor basins west and north of Mohave River are "post-Lahontan" and belonged to the Mohave drainage.

Three of these basins had sufficient drainage to form Pluvial lakes. The largest of these lakes (no. 57A), of which only the northern tip is included on our map, was roughly mapped by Russell (1885) and, more accurately, by Meinzer (1922) and was named Lake Thompson by Miller (1946*a*: fig. 1, no. 19). It occupied Rosamond, Buckhorn, and Rogers (or Muroc) Dry lakes in Antelope Valley, Kern and Los Angeles counties, California. There is evidence, suggested by Thompson (1929: 302–304) and confirmed by Hoyt S. Gale (in Miller, 1946*a*: 53), that Lake Thompson discharged northward into Lake Kane (no. 57B), but no definite indications that either of these lakes overflowed eastward at any Pluvial time across the intervening height of land into the Mohave River system or into the basin of Pluvial Lake Harper (57C). That lake was also briefly described by Thompson (1929: 270), who (p. 426) postulated that Mohave River, during a higher stage, may have flowed for a time into Harper Valley to form a lake. It is conceivable that this could have happened during stage I of Lake Manix (p. 87) when, prior to the draining of that basin, Mohave River must have stood at a higher level. On the other hand, the former elevated course of the river may date back to an "earlier pluvial" period. A cursory examination of the region did not provide any clear confirmation of Thompson's supposition. North and east of Lake Harper lie a succession of small desert basins, each now draining into a playa. These basins are mapped under the general designation 57D in accordance with the Recent drainage pattern as determined by Thompson (1929). So far as known each of these basins was also independent in Pluvial time, but the Pluvial drainage relations here are highly problematical. General topographical relations suggest that these basins in some Prepluvial time were a part of the Mohave River system.

58.—Lakes between Death Valley System and Fish Lake Valley

North of Panamint Valley and east of Owens Valley, in the northern half of Inyo County, California, is a generally inaccessible area comprising four arid and wholly enclosed basins which contained at least ephemeral lakes during Pluvial times. These are, from north to south, Deep Springs Lake, Lake Eureka, Saline Lake, and Butte Lake. We have visited only the Deep Springs and Saline valleys, both of which now contain large playas that are still filled during heavy rains.

A.—DEEP SPRINGS LAKE.—Deep Springs Valley, the northermost of these four basins, was probably never reached by fish, though a moisture-loving toad which we discovered there has been described as an endemic form by Myers (1942). This remarkable fault-block valley contains lacustrine playa deposits indicating the former presence of a lake, which may be called *Deep Springs Lake*. This body of water may or may not have been permanent. It possibly overflowed in an "earlier pluvial" period, but not in "Lahontan time," as was claimed by Free (1914*a*). Any discharge would have been into the much lower, wholly enclosed Eureka Valley, just west of the north end of Death Valley. We cannot agree with Miller (1928), however, that Deep Springs Valley was occupied by a deep lake in late Quaternary time, since no indications of shore features to support that hypothesis have been reported or seen by us. Much less can we agree with Miller's idea that the rounded boulders along the high, sharp eastern rim represent a former continuation of Wyman Creek, which now flows into the northwestern end of Deep Springs Valley. This valley is habitable for fish, for it contains live spring water in which introduced species have multiplied. Its lack of native fish life is probably due to the circumstance that none ever gained entrance.

B.—EUREKA LAKE.—Concerning the second of these fishless basins in California, Chalfant (1936: 68) wrote that "Eureka Valley, twenty-mile depression neighboring Death Valley's northern arm and just now the scene of sulphur-mining operations, is without a single source of water." The valley, therefore, is to be regarded as fishless now, as it probably was also in Pluvial times, when it was supposed by Bailey (1902) and by Free (1914*a*) to have contained a lake. No great reliance, however, is generally placed on the opinions of these authors. Bailey named the supposed water Eureka Lake.

C.—SALINE LAKE.—Saline Valley, located just south of Eureka Valley, and separated by the Inyo Range from Owens Valley to the west, is another completely enclosed basin which is wholly fishless (Miller, 1944), despite the fact that it contains permanent, apparently habitable, surface waters, and has been thought by at least one geologist (Bailey, 1902) to have been the site of a Pluvial lake. Bailey named this supposed Pleistocene water Saline Lake.

D.—BUTTE LAKE.—This is another supposedly Pleistocene lake that was named Butte Lake and mapped as Butte Valley Lake by Bailey (1902). At least at the size he indicated, it was probably of "earlier pluvial" age. The valley was figured by Shuler (1945: fig. 31 on p. 65) as a typical enclosed desert basin. Free (1914*a*: 41) indicated that this basin (the "Racetrack"?) was previously tributary to Saline Valley, but has been cut off by stream decay and alluvial damming.

59.—Lakes between Death Valley System and Colorado River

A considerable number of separately enclosed basins lie in the desiccated area between the Death Valley system and the Colorado River. Nearly all contain a playa that may be the remnant of a more or less permanent Pluvial lake. The region probably remained too arid, however, to have developed deep lakes at any Pluvial time. All of the basins are now fishless. The lakes that lay in and near Nevada (Lake Mesquite, no. 59A; Lake Ivanpah, 59B; and 3 unnamed lakes, nos. 59C–E) are shown with drainage divides on map 1, in accordance with the topographic maps of the United States Geological Survey and the Metropolitan Water District. The more southerly lakes are shown on the maps by Thompson (1929) and by Miller (1946*a*). These waters are listed, with references and locations, on pages 163–164. We apply the name *Lake Lucerne* (no. 59*d*) to the possibly ephemeral lake mapped by Hay (1927) in the position of the dry lake in Lucerne Valley.

Two southern lakes in this group have been designated as Pleistocene: (1) Lake Amboy (no. 59*a*; tributaries labeled F on map I), in the Bristol–Cadiz dry-lake basin, and (2) Lake Ward (no. 59*d*), in the Danby dry-lake basin. Both are in San Bernardino County, California, and both were described and named by Thompson (1929: 696, 708). These lakes are of particular interest in that they lay along a plausible course of the ancient, probably "earlier pluvial," discharge from the Death Valley system into Colorado River (Blackwelder, 1933, 1934; Blackwelder and Ellsworth, 1936; Miller, 1946*a*: 50–52). Various other lakes (no. 59*c*) in the same region were probably ephemeral.

Lake Ivanpah (map 1, no. 59B), which Bailey (1902) indicated on his map as a former large body of water near the California–Nevada boundary south of Las Vegas, was, in our opinion, never more than a shallow lake during Pluvial times and probably then occupied an area little larger than its present playa bed (Miller, 1946*a*, fig. 1, no. 13).

60.—RAILROAD LAKE SYSTEM

In the central part of Nevada lies a complex of valleys which in Pluvial times comprised the drainage basin of Railroad Lake (map 1, no. 60; Fig. 23), one of the larger of the ancient seas. Like the Death Valley system in California, the Railroad Lake system intervenes between the watersheds of Lake Lahontan and of the Colorado River and harbors fishes that are related to those of both major drainages.

Our field observations, confirming the brief statements by Free (1913, 1914*a*) and by Carpenter (1915) and the map of Lee, Stone, Gale and others (1915), indicate that this drainage basin covered about 6,000 square miles of now arid land, lying a little to the south and east of the geographic center of Nevada. To the northwest and north lie Monitor, Antelope, Little Smoky and Newark valleys, which contained Pluvial tributaries of Lake Lahontan. To the east lies the drainage basin of Pluvial White River, a former tributary of the Colorado, and to the south and southwest lies the Area of Sterile Basins, with almost no surface water and no trace (as yet discovered) of fish life.

The fishes of the Railroad Valley system are of two species. One (Fig. 24) is *Crenichthys nevadae* Hubbs (1932), a relative of *Empetrichthys* of the Death Valley system. The only other known species of *Crenichthys* is *C. baileyi* (Gilbert), which inhabits the now disrupted segments of the Pluvial

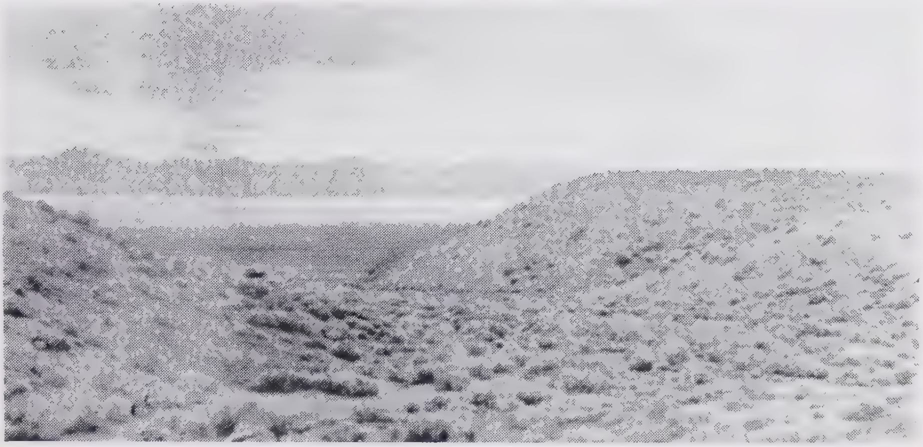

Fig. 23. Pluvial Railroad Lake, Nevada, represented by broad playa and by immense gravel bar. Note automobile. Looking westward toward Reveille Range.

White River system, and is therefore a member of the Colorado River fauna (Hubbs and Miller, 1941). *Crenichthys nevadae* inhabits hot springs in Railroad Valley and the tributary Duckwater Valley.

The second species of fish in Railroad Valley is *Siphateles obesus.* This species is especially characteristic of the Lahontan system, but occurs also in the Sacramento, Klamath and Columbia river systems, and in the isolated lakes that lie between those systems and the Lahontan basin. There are other forms of *Siphateles* in the Death Valley system, as already mentioned, but none is known from any Recent or Pluvial tributary of the Colorado River. We therefore assume that the Railroad Valley system probably received its *Siphateles* from the north, possibly through stream capture or stream wandering on the alluvial saddle between the southeast arm of Newark Valley and either the Bull Creek or the Duckwater arm of Railroad Valley. The theory of passage across either of these divides is more plausible than that of a transfer across the low pass (Free, 1914*a*) between Fish Creek and Hot Creek valleys, because a separate basin, Sand Spring Valley, with a small dry lake, occurs on that divide. In lava hills on the east side of Pancake Mountains, along the west side of Duckwater Valley, a series of canyons slopes northward toward the alluvial divide between this valley and Newark Valley, and may once have drained that way, though the flood waters now cut back into Duckwater Valley. Such a change in drainage would bring fish from the Lahontan into the Railroad system.

When Railroad Valley contained the large Pluvial Railroad Lake (Carpenter, 1915; Hubbs, 1941*a*) and a number of live tributaries, all of the chubs in the basin were probably of a single kind. As the Postpluvial aridity isolated fragments of the former lake and stream system, local differentiation set in, so that we now class the chubs of the Railroad Valley system in 8 subspecies, each occupying a single spring or a small group of springs. Some of these home ranges are almost unbelievably close to one another, lying in the same intermittent creek course or watering the same meadow area. Other habitats are separated by long stretches of desert, yet the close similarity of the isolated subspecies confirms the physiographic evidence of the former continuity of the waters. This is strikingly true of the three very similar subspecies inhabiting respectively the springs of Fish Lake Valley, Twin Springs in Warm

Springs Valley and Duckwater Creek in the northwest arm of Railroad Valley. Fish Lake Valley, far to the north and west, slopes toward Hot Creek, which is now much too hot for fish life except perhaps in periods of great flood. Hot Creek flows in a very deep canyon through the Hot Creek Range, and thence out into Hot Creek Valley. A normally dry arroyo then traverses that valley and its continuation, Warm Springs Valley. Near Twin Springs the flood-water arroyo of Warm Creek Valley passes into and through a canyon (Twin Springs Pass or Slough) that separates the Pancake and Reveille ranges. The drainage line thence extends to the southwest corner of the playa in Railroad Valley. Flood waters from Twin Springs rather than, as locally held, underground waters, presumably carried the chubs that rapidly populated the overflow of Artesian Well 7 in Railroad Valley. Extreme floods may still connect the discharge from Warm Springs Valley with that from Duckwater Valley, along the west side of the bed of the Pluvial Railroad Lake. Connections can thus be traced between fish populations in the now isolated fragments of a formerly continuous river system. Again the geological and the biological evidence find mutual support.

Since at present the dry bed of Railroad Lake never fills with water, the occasionally connected waters on the west side of the valley do not at any time join with the springs on the east side. That such a connection may have existed during some Postpluvial wet period is faintly suggested by Indian legend. Some years ago "Morey Jack," a well-known local Indian, when 93 years old, told Mr. H. Titus (in charge of the Railroad Valley Wildlife Refuge) that his father told him of having heard his father telling of swimming in the now perennially dry bed of Railroad Lake. If this be true, the speciation of chubs in the springs on the east side of the valley may be very recent.

The drainage channel from Fish Lake Valley to Railroad Valley was undoubtedly once followed by a permanent stream, which may be known as *Pluvial Russell River,* as a slight remembrance of Israel Cook Russell's monumental contributions to Great Basin hydrography. This stream was obviously of ancient origin, for the canyons which it follows through two mountain ranges presumably could not have been cut during Pluvial and Postpluvial (that is, Wisconsin) time. Russell River appears to be antecedent to the mountains, but the canyons may have been cut by the accelerated erosion on the eastern fault escarpment of the two mountain ranges, according to the explanation favored by Gilbert (1928) for somewhat similar drainages across the Wasatch Mountains. By whatever means it may have become integrated, Russell River was the main tributary of Pluvial Railroad Lake. It may well represent the upper fragment of an ancient (early Pleistocene?) river that was tributary to Colorado River, or that was in some other way connected with the precursor of Pluvial White River. These conclusions harmonize with the occurrence of one species of *Crenichthys* in Railroad Valley and of another throughout the remnants of Pluvial White River, and with the restriction of this fish genus to these two water systems.

What course the presumed "earlier pluvial" stream may have taken from Railroad Valley to the Colorado River is not certainly determinable, but is strongly suggested by the physiographical as well as the ichthyological evidence. Although no through river channels remain, there is a structural connection by way of Penoyer and Desert Valleys (p. 50; map 1, nos. 23W and 23Y). The lowest divide out of Railroad Valley is from its south end into Penoyer Valley, which is separated by a rather low divide from Desert Valley, which in turn opens across a rather low divide into Pahranagat Valley of the Pluvial White River system.

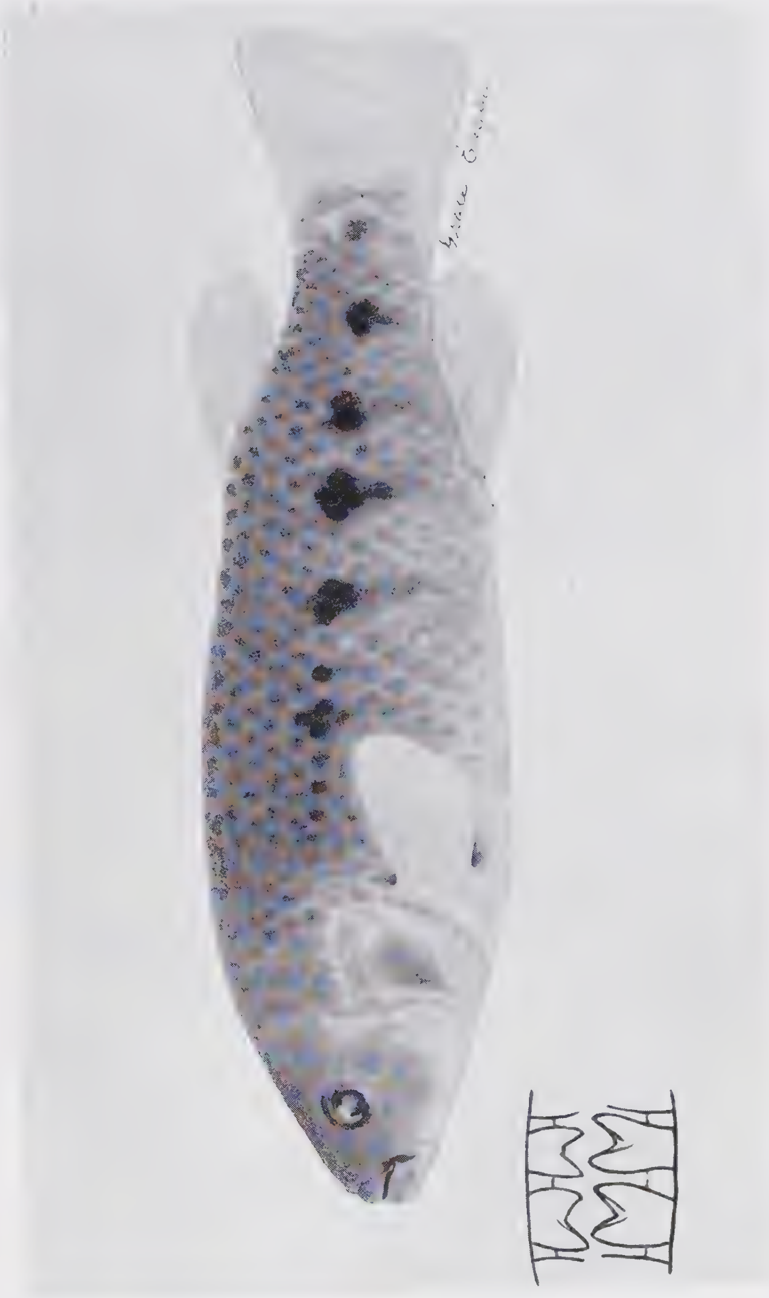

Fig. 24. **Crenichthys nevadae** Hubbs, a cyprinodont fish confined to the warm springs of Railroad Valley. The only other species of **Crenichthys**, **C. baileyi** (Gilbert), characterizes the remnants of Pluvial White River.

Other drainage relations in and about the southern part of the Railroad Lake basin are clearer. The dry area south of Warm Springs Valley and to the west of the Reveille Range, shown on most maps as Reveille Valley, drains both to the north and to the south, but both courses flow to Railroad Valley. The northerly course leads into Warm Springs Valley and thence through Twin Springs Pass into the main depression of Railroad Valley. The southern part of the valley flows around the south end of the Reveille Range and then, with the drainage from the extreme northern part of Kawich Valley, empties into Reveille Dry Lake in the southern part of Railroad Valley. Reveille and Railroad dry lakes, however, are separated by only a very slight alluvial rise, and very probably had a Pluvial connection. Structurally the dry Kawich Valley (see Kawich Quadrangle, U. S. G. S.) is the southward continuation of both Reveille and Railroad Valleys, and it may have had a Prepluvial connection with Railroad Valley. Kawich Valley, like Railroad Valley, is a deeply enclosed basin (p. 50). It contains Kawich Dry Lake, which lies about 400 feet below the pass into Railroad Valley. Kawich was obviously a separate Pluvial basin (map 1, 23V), and it may well have contained a sizeable Pluvial lake. Free's theory (1914*a*) of "a Lahontan period drainage" from Kawich Valley to Railroad Valley is certainly untenable. Kawich Valley in turn is trenchantly separated by Pahute Mesa from Forty-mile Canyon of the Amargosa drainage and other dry drainages to the southward (Chapman, 1906). The intervening country is said to be difficult to cross on account of rimrock. Gold Flat, a sterile basin, lies beyond the Kawich Range to the west and Kawich Valley is bordered on the east by the Belted Range. It therefore seems unlikely that Kawich Valley is a part of any former drainage of Railroad Lake.

DISRUPTED PARTS OF THE COLORADO RIVER SYSTEM

In the uncertain boundary area between the Great Basin and the Colorado River system, just south and east of the Area of Sterile Basins in Nevada (p. 45), there are located the remains of at least three Pluvial rivers that were tributary to the Colorado River. Traversing a region of extreme aridity, these stream systems have become reduced to fragments that are now connected only in times of desert cloudbursts and probably never carry water at any one time throughout their entire length. These water courses seem to come to life, however, when we study either the physiographic evidence of their former channels or the relict fish life of the remaining springs and brooks. Other parts of the Colorado River drainage, from Wyoming to the Gulf of California, have also become disrupted.

The zoological facts harmonize with the view that the Colorado River system was well integrated, hydrographically and faunistically, in late Pleistocene (Pluvial) time. Colorado River types of fishes occur in isolated waters which are indicated by the physiographic evidence to have been parts of this great stream system.

The distinctiveness of the Colorado River fish fauna, including as it does 8 endemic genera out of 19 (Miller, 1946*b*), bespeaks a long and continuous history. A similar conclusion was reached by Gilbert and Scofield (1898: 487–488) from a study of the Colorado River fishes and by Grinnell (1914) from a study of the riparian birds and mammals. Such evidence conflicts in general with the provisional hypothesis of Blackwelder (1934) that the whole existence of the Colorado River, and with it that of the Grand Canyon, may date only from the Pleistocene. There is certain faunistic evidence, however, which favors the theory that the present Colorado River system and fauna are the product of the amalgamation of several elements. There are wide distinctions between the fish faunas of (1) the upper headwaters in Wyoming and Colorado, (2) the middle portion of the system, (3) the Gila River division (including the Williams River), and (4) the Pluvial White River.

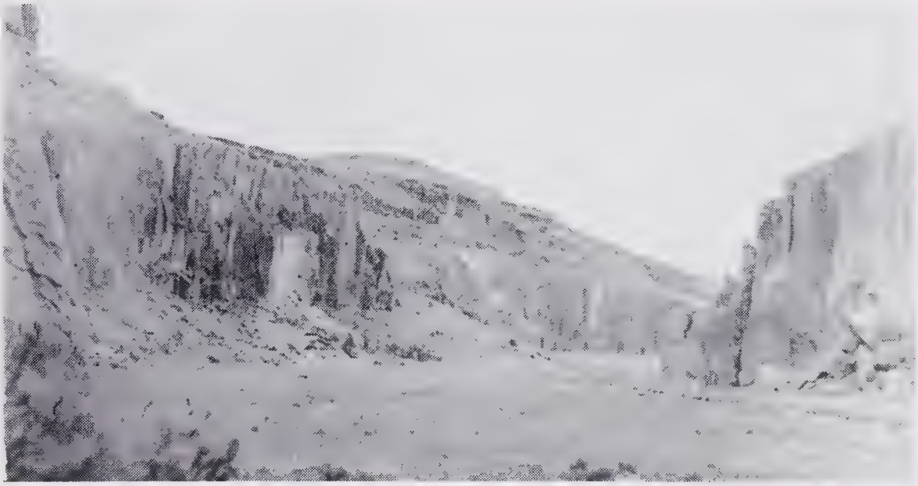

Fig. 25. Now dry course of Pluvial White River, above Hiko Spring, Nevada. The white streak is a road. Indian pictographs (Fig. 28) occur on the right wall.

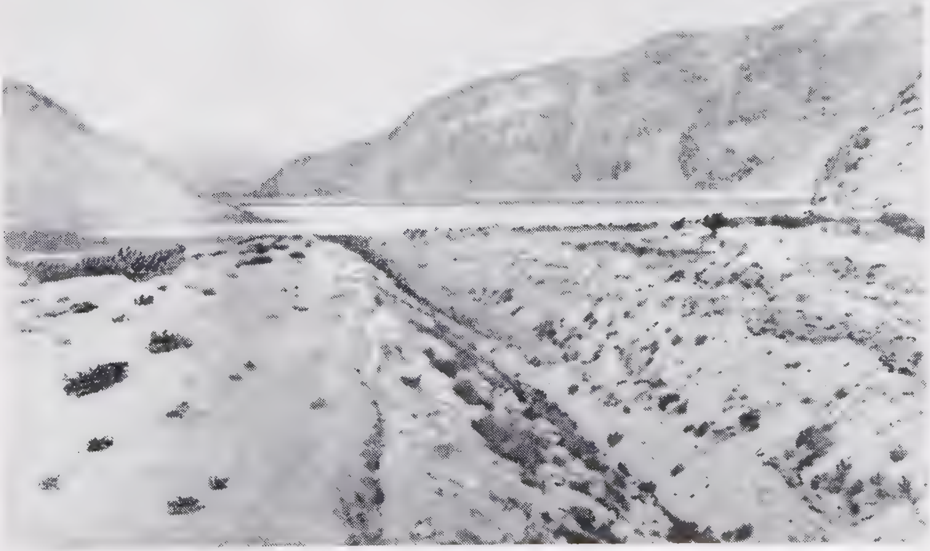

Fig. 26. Maynard Lake in course of Pluvial White River, just below Pahranagat Valley, Nevada. The trench is cut in the alluvial dam formed by the outlet of Pluvial Lake Delamar.

61–64.—**Pluvial White River and Probably Connected Lakes**

When in 1934 we first dipped our nets in the tiny White River in east-central Nevada, above Preston, we at once realized that we were sampling an isolated remnant of the Colorado River fauna. Somehow, we felt sure, the precursor waters of White River (map 1, no. 61) must once have traversed the nearly 200 miles of parched desert that now intervene between the Recent White River and the Colorado. Later we noticed that Gilbert (1893: 231) had already come to a similar conclusion, when he found the Colorado River cyprinid genus *Lepidomeda* in Pahranagat Valley, which lies about midway in the ancient drainage. We also found that Carpenter (1915) had traced the Pluvial course of White River clear through to the short Moapa or Muddy River, a present tributary of the Virgin and Colorado rivers that is kept alive by large warm springs. Since then we have seen almost the entire course of this Pluvial river, travelling much of the way on a trail that was built in the dry river bed (Fig. 25). Everywhere we have confirmed Carpenter's interpretation. The only section we missed is that between Coyote Spring Valley and Arrow or Arrowhead Canyon (Hubbs, 1941*a*: fig. 7), the narrow trench (Fig. 27) through which the ancient river poured to reach Moapa River. Dr. Chester R. Longwell, who kindly re-examined this region for us, provides the final confirmation of Carpenter's view. Local testimony is fully consistent with his findings. Hydrographic relations in this region are indicated by Youngs and Carpenter (1928), Longwell (1928) and Harrington (1930), and are well shown on the Plan of Muddy River, Nevada, published by the U. S. Geological Survey in 1937. An examination of the area with binoculars from an airplane in 1947 confirmed the drainage course from Coyote Springs Valley to the Moapa River.

The spring and brook fragments of the Pluvial White system can be tied together as conclusively by the evidence of their fish populations (Hubbs, 1941*a*; Hubbs and Miller, 1941) as by the physiographic data. The fragmentation of the river system has been accompanied by rather extensive subspeciation of the isolated fish populations. Some of these segregates occupy distinctive habitats in close proximity.

The fishes of Pahranagat Valley, midway in the course of Pluvial White River, were described by Gilbert (1893). Hot-spring fishes of White River Valley have been studied from a physiological standpoint by Sumner and Sargent (1940) and by Sumner and Lanham (1942). One of the White River fishes has been named recently by Tanner (1942); others remain to be named.

The White River fish fauna is highly distinctive. It includes a unique genus of the minnow family, Cyprinidae (Hubbs and Miller, in press); an endemic species of *Crenichthys,* which genus is further known only from Railroad Valley (p. 90); and a number of indigenous species and subspecies. These peculiarities suggest that the White River fauna was long isolated from that of the Colorado. One isolating factor has presumably been the tempestuous current of the Colorado River in the Grand Canyon area (prior of course to the construction of Hoover Dam). This condition would explain why the fauna has remained isolated through Recent times despite the fact that the lower end of the system, the Moapa River, still flows into the Colorado. The distinctive environmental features of Moapa River may be another isolating factor. The peculiarities of the White River fauna may, however, date from the early isolation of the White River system. There is evidence that neither the Virgin River nor the Colorado River existed in this region during the Pliocene (Longwell, 1928; Blackwelder, 1934). Then, and perhaps in early Pleistocene, White River may have been tributary to the isolated lake that laid down the

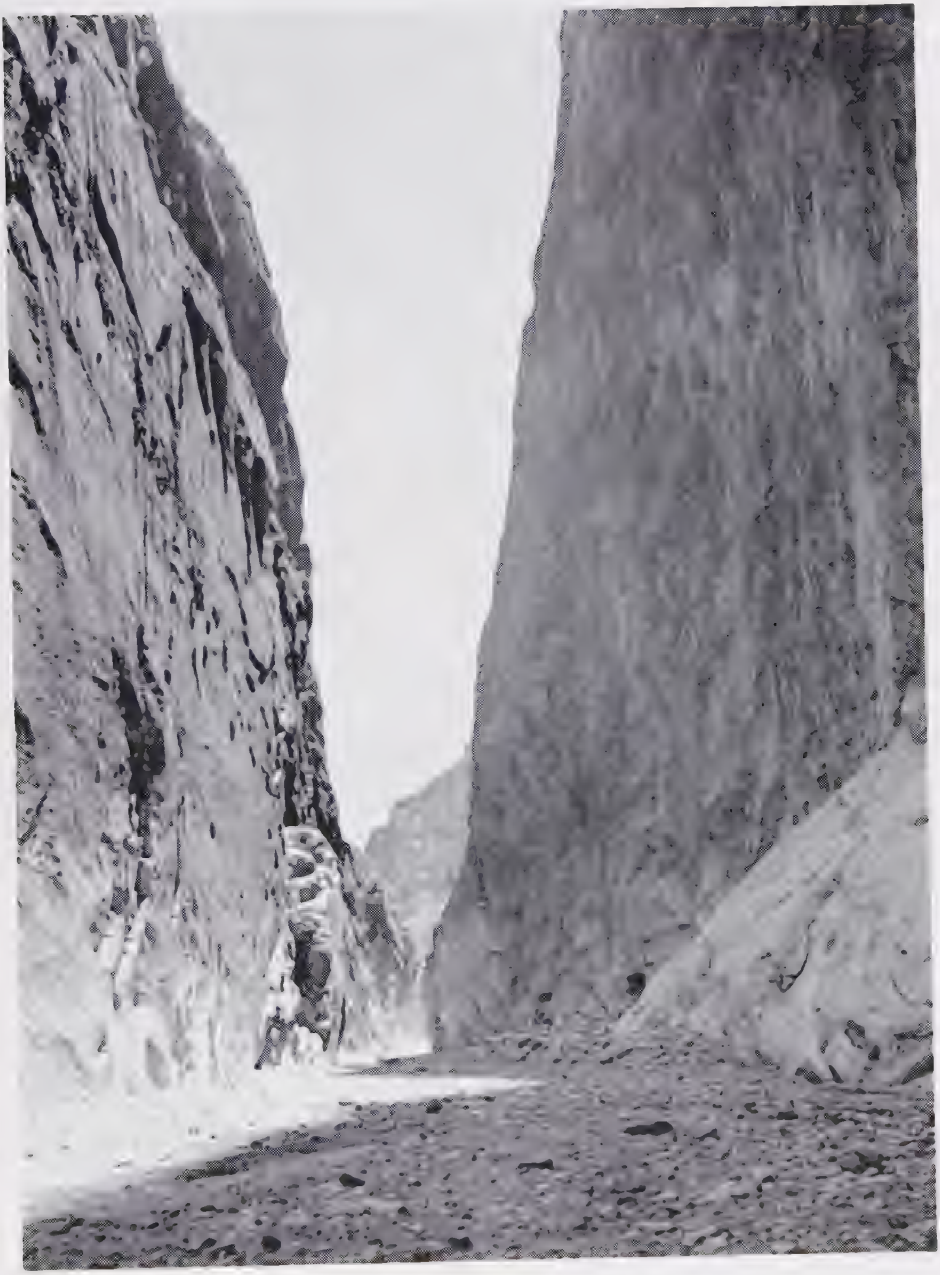

Fig. 27. Arrowhead Canyon, Nevada, in the course of Pluvial White River, above the spring sources of Moapa River.

extensive lacustrine beds of chalk and clay now entrenched by the Moapa River and tributary draws near Moapa. We understand that fish remains have been taken in these chalk deposits. When these fossil fishes have been studied, more light may be thrown on the history of the White River fauna.

Adjacent to the long, tortuous and now generally dry course of Pluvial White River are a series of valleys, set off only by alluvial divides. Carpenter (1915) interpreted these valleys as portions of the Great Basin, because the Pluvial lakes (in Coal, Bristol and Delamar valleys; map 1, nos. 62, 63 and 64, respectively) gave him no evidence of outlets. They may well have supplied tributaries, however, to a White River of "earlier pluvial" periods. Or they may have had brief Pluvial outflows. Evidence was found by us of a discharge into White River, during either Pluvial time proper or one of the later of the "earlier pluvial" periods, from Delamar Valley, and perhaps from the structurally continuous Bristol Valley (these two valleys are commonly labelled Dry Lake Valley or Desert Valley). At the mouth of the side canyon leading from Delamar Valley (see Carpenter's map) the larger canyon of White River is filled by a high dam of coarse, unconsolidated stream alluvium (Fig. 26). This barrier, which was referred to by Gilbert (1875*a*: 112), produced Maynard Lake, the lowest of the chain of Pahranagat Lakes. Free (1914*a*) expressed the opinion, without supporting evidence, that, during the "Lahontan period," the Colorado River system received the discharge of "Desert Valley" (=Delamar+Bristol valleys; not the Desert Valley of many maps (no. 23 Y on map 1), which lies in the Area of Sterile Basins west of Pluvial White River, across the Pahranagat Range). Fifteen miles below Maynard Lake, strong Pluvial terraces along Kane Springs Wash indicate that White River received a tributary from another valley on the east side. The lower part of White River, in the course of Recent Moapa River, received flood waters from another terraced valley, that of California Wash, from the southwest. That tributary had a common divide with the Las Vegas River system. In this way the Area of Sterile Basins was cut off from the Colorado River (see map 1). Cave Valley, just south of Steptoe Valley, was probably also once tributary to White River, for it is said to end in a dry lake bed that is separated by only a slight alluvial saddle from the White River canyon; but whether such a connection existed in Pluvial time is unknown. Cave Valley contains fine live springs and short but permanent creeks, but unfortunately neither this valley nor Garden Valley has yielded any fish specimens. Garden Valley contains live streams, leading to the waterless Coal Valley (site of Coal Lake) by way of an obviously ancient channel (now dry) through Golden Gate Range. As described by Carpenter the other side valleys contain no permanent water. Local testimony unanimously indicates that all the valleys adjacent to the course of Pluvial White River are wholly fishless.

Several valleys that we include in the Area of Sterile Basins were probably once tributary to White River, but at an "earlier pluvial" time. These fishless basins are treated on pages 50–51.

65–66.—**Pluvial Carpenter River and Lake Carpenter**

Intervening between and paralleling the Pluvial White River and the Nevada–Utah border another Pluvial stream course threads its way between desert hills. This channel joins the Moapa or Muddy River (the lower portion of the Pluvial White River) near the railroad station of Moapa. The main portion of the course is properly known as Meadow Valley Wash, though on most maps, including the Nevada base map of the U. S. Geological Survey, its lower end is misnamed Muddy River. Since this stream course (map 1, no. 65)

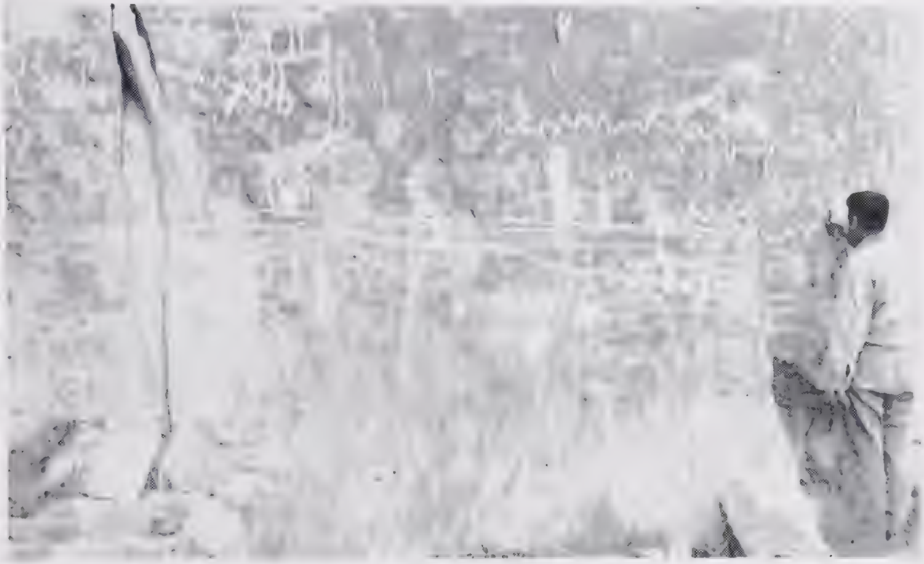

Fig. 28. Indian pictographs on wall of dry channel at Pluvial White River (Fig. 25)

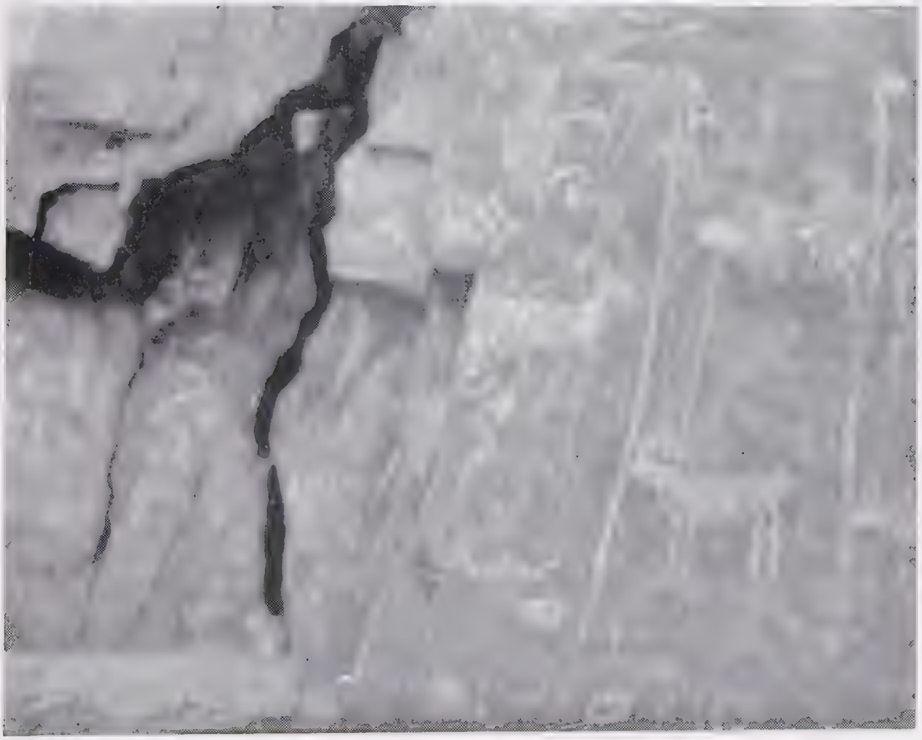

Fig. 29. Indian pictographs on canyon wall at mouth of Arrowhead Canyon (Fig 27)

is one of considerable magnitude and contains a uniform and distinctive fish fauna, we think it should be named. The designation, *Pluvial Carpenter River,* is suggested, to commemorate the excellent hydrographic researches of Everett Carpenter on this stream system and that of the Pluvial White River.

One of the upper branches heads in Camp Valley and drains through a chain of small valleys and canyons to join the western branch, which heads in Duck or Lake Valley. That valley is the site of an ancient lake (map 1, no. 66), for which we suggest the name *Pluvial Lake Carpenter,* since this lake as well as its outlet into Pluvial Carpenter River was described by Carpenter (1915). Duck Valley is structurally continuous with Spring Valley of the interior drainage west of Wheller Peak (p. 56), but the two basins are separated by a low divide of igneous hills ("Fortification Mountains"). Springs in Duck Valley yielded Utah chubs, *Gila atraria,* but these are said to have been brought in by Mormon settlers (Miller and Alcorn, 1946: 182). The eastern branch and the main channel contain short stretches of live water, from Camp Valley to the canyon mouth above Moapa. This branch and Meadow Valley Wash below yielded 3 endemic fishes, including a species of the exclusively Colorado genus *Lepidomeda.* This small but highly distinctive local fauna has somehow managed to persist in this stream system despite the destructive floods that occasionally scour through Meadow Valley Wash (Pack, 1939). At such times Pluvial Carpenter River is temporarily revived. Since these floods continue to the Colorado River (now to Lake Mead) they might be regarded as a means by which the permanent parts of Meadow Valley Wash would become stocked with typical Colorado River fishes. Following the great flood of 1938, however, we failed to find evidence of any such contamination of the Carpenter River fauna. Probably the brief rush of the floods is too torrential to be stemmed by the fishes, and the cessation of the floods is too sudden to permit an upstream migration.

That the ancient White and Carpenter rivers were Colorado tributaries of large flow and long standing is attested by the well-developed terraces that line their lower courses, slicing the mountain sides far above the present stream beds. The size of the valley that lies between their junction and the Virgin River confirms this interpretation. We cannot subscribe, however, to the aberrant theory of Keyes (1917–1918) that this valley represents the course of an "Old Virgin River" that arose in the Yellowstone region and continued as a through-flowing stream along the upper Snake River and across the Bonneville basin. There are great terraces along the lower course of Carpenter River which the "Old Virgin" would have followed, but there are also concordantly large terraces along the lower White River. Both rivers must have been larger because of greater precipitation. Keyes' ideas fall down both on hydrographic data (p. 31) and on ichthyological evidence (p. 22).

Speciation of fishes within the dwindling remnants of the Pluvial White and Carpenter rivers suggests long isolation. We cannot be sure, however, that all of this speciation has been correlated with the Postpluvial disruption of these rivers from the Colorado, because Virgin River, which still maintains its connection with the Colorado, except in dry portions of the year, also contains a series of endemic subspecies.

67–69.—**Pluvial Las Vegas River and Probably Connected Lakes**

In the arid Las Vegas Valley, lying to the southwest of Pluvial White and Carpenter rivers in Nevada, there is physiographic evidence of another river which maintained a Pluvial flow south to the Colorado River. This stream we call *Pluvial Las Vegas River* (map 1, no. 67). Las Vegas Creek occupies a small part of the former river bed. The ancient stream course as well as the present flood channel can be traced from the southeastern part of Las Vegas Valley through a well-defined channel (Las Vegas Wash) and thence through a deep rock canyon into the Colorado River (Carpenter, 1915). This wash provides the only exit for surplus waters in the Las Vegas Valley (Carpenter and Youngs, 1928). Large sloughs along this channel further mark the old drainage, which is still occasionally followed by flood waters. These drainage relations are particularly obvious in air view.

There is evidence that a lake or a series of ponds temporarily existed in Pluvial, or more likely in Postpluvial, time over an undetermined portion of the Las Vegas Valley. Lake beds presumed to be Pleistocene (Rose, 1938) have yielded pond snails and fossil mammals along with evidences of human occupation (Simpson, 1933). Harrington (1934*a* and verbal communication) has indicated that the remains of an Indian camp site near Tule Springs, just north of Las Vegas, are covered by a lacustrine deposit abounding in small clam shells. The topographic relations in the region, however, argue against the existence here of a Pluvial or Postpluvial lake of any considerable size, depth or permanence.

Lying within the northwestern extension of the structural trough connecting Las Vegas Valley with the Amargosa drainage of the Death Valley system are two basins which contained Pluvial lakes (Carpenter, 1915). The first of these, now dry except during floods, was occupied by a small lake (map 1, no. 68C) which had an outlet into Las Vegas Valley. For this body of water, located about 36° 35′ N. Lat., 115° 30′ W. Long. (about 35 miles northwest of Las Vegas), we propose the name *Pluvial East Lake,* because the present remnant is known as East Lake (a playa). This lake occupied the lower end of Mormon Gulch or Three Lakes Valley. Farther up, between the Desert and Pintwater ranges, are two other playas (nos. 68A and 68B) which in the Pluvial were probably interconnected and probably discharged regularly into East Lake. Local testimony was uncertain as to whether such connections are now established during floods.

The second basin, about 5 miles west of the first, is known as Indian Springs Valley. *Pluvial Indian Springs Lake,* as we propose to call the sizeable body of water (map 1, no. 69) that Carpenter (1915) indicated as having once accumlated here, apparently reached no permanent outlet, despite the fact that alluvial saddles of no great height are all that separated this basin from that of Las Vegas River (via East Lake) to the south and from Amargosa River to the west. Free (1914*a*) indicated a rather recent discharge to the south but the physiographic evidence, as well as the lack of fish in Indian Springs, argues against his view. A very brief Pluvial or an "earlier pluvial" discharge may of course have occurred in that direction. Because of this strong possibility and of other physiographic relations and because of fish distributional data mentioned below, we treat Indian Springs Valley in connection with Pluvial Las Vegas River.

There is physiographic evidence for a possible connection across the alluvial divide separating the Indian Springs and Amargosa basins (Gilluly, 1929: 682). An area of about 150 square miles between Charleston and Point of Rocks in Nevada (see U. S. G. S. Las Vegas and Furnace Creek quadrangles) was formerly tributary to Indian Springs but has been captured by a branch of Amargosa River. While the divide was migrating eastward one or more creeks within the Indian Springs basin may have become diverted into the Amargosa.

The physiographic facts and conclusions regarding Pluvial Las Vegas River find some corollaries in the ichthyological data. The occurrence of a species of fish (a *Rhinichthys*) in Las Vegas Creek and in springs near by calls for a former connection with some other water containing fish of the same general type. The Colorado River system satisfies this need. The fact that in some respects the Las Vegas *Rhinichthys* is the most extreme of the multitudinous forms of *Rhinichthys osculus* calls for a long period of isolation dating back at least to Pluvial time. It is unfortunate that only the one kind of fish is native in Las Vegas waters and that it belongs to a species that is very widely spread.

Another correlation exists between the ichthyological and geological data. The extreme form of *Rhinichthys* in Las Vegas Creek is approached rather definitely by *Rhinichthys osculus nevadensis* of the Amargosa River (Ash Meadows) in the Death Valley drainage (p. 84). The two forms look so much alike that the first-taken samples were both referred to *R. nevadensis* by a critical ichthyologist (Gilbert, 1893). The similarity between the fishes of the two drainages and the indicated capture of a portion of the Indian Springs basin by a tributary of the Amargosa River (p. 101) led one of us (Miller, 1946*a*: 49–50) to conclude that the *Rhinichthys* of the Amargosa River, unlike the subspecies in other parts of the Death Valley complex, was derived from the Las Vegas River system. This conclusion is plausible, though it calls not only for a postulated stream transfer across the migrating divide but also for the former occurrence and later extirpation of the Las Vegas *Rhinichthys* in the Indian Springs basin. There is no evidence that this fish occurred in that basin and indeed, as we have said, no clear indication of a Pluvial connection between the Indian Springs and Las Vegas basins. It is true that Gilbert (1893), in his report on the fishes of this region, recorded *R. nevadensis* from "Indian Creek" as well as from Las Vegas and from Amargosa River, but we learned from the field records of Vernon Bailey, that the Indian Creek Gilbert mentioned is a Reese River headwater tributary (of the Lahontan basin) that abounds in *R. o. robustus*. The lack of native fish life in Indian Springs is surprising, for these springs maintain a large flow of pure water and lie on the basin floor. It is possible that native dace were once present but have been eliminated by introduced fish. The transfer of fishes from Las Vegas to Amargosa waters may have taken place at an "earlier pluvial" time.

Trout occur or have occurred in several small cool spring creeks in the Las Vegas drainage on the east side of the Spring Mountains, which include lofty Charleston Peak. All indications, however, point to the conclusion that these fish were introduced.

Northeast of the Indian Springs–Las Vegas trough lies the Area of Sterile Basins, some of which may once have drained into the Colorado through this trough, as Free (1914*a*) hinted. These drainage relations are discussed on p. 49.

69*a*.—**Lake Pinto and Pinto River**

Some distance south of the Las Vegas trough and between the Mohave and Colorado deserts lies the Pinto Basin (shown south of lakes 20 and 21 on the map by Miller, 1946*a*). It is located in the Joshua Tree National Monument, Riverside County, California. This depression is surrounded by desert ranges, except at the southeastern corner. During Pleistocene time, a large lake (which may be called *Lake Pinto*) occupied this basin and perhaps also that of the near-by Chuckwalla Valley (Scharf, 1935). Presumably Lake Pinto was of "earier pluvial" age as its deposits have been well dissected and its shore features largely erased. At a later time, after the disappearance of Lake Pinto, the sluggish Pinto River occupied the upper terrace of its present remnant, Pinto Wash. During the existence of this presumably Pluvial river, a primitive people camped along its banks (Campbell and Amsden, 1934; Campbell and Campbell, 1935; Scharf, 1935; Rogers, 1939). Whether this river or its lacustrine predecessor had a connection with the Colorado River is not definitely known, although Free (1914*a*) claimed that Mesquite Trough (containing the Recent playas of Mesquite, Dale and Palen lakes) was tributary to the Colorado quite recently. The basin of Palen and Ford dry lakes (in Chuckwalla Valley), to which Pinto River was directly tributary, is separated only by a low alluvial saddle from the Colorado River basin about 12 miles west of Blythe. A Pluvial discharge over this saddle seems very plausible. We have not visited Pinto Basin, but the published descriptions of this arid region suggest that it is devoid of fish life.

69*b–c*.—**Lakes LeConte, Clark and Pattie**

We treat as intermittently disrupted parts of the Colorado River system two basins that are separated from the Gulf of California by the massive delta of the Colorado River. Their hydrographic history is intimately connected with that of the Colorado, for their lake beds have been dry except during the periods when they have been partly to wholly filled by distributary flows from that river. The relations of these basins to one another, to the river and to the Gulf of California have been most comprehensively treated by Kniffen (1932) and by Sykes (1937).

69*b*.—LAKE LECONTE.—The more northerly of these two basins drains toward or into a depression, lying below sea-level, that is variously known as the Colorado Desert or as part thereof, as Cahuilla (or Coahuila) Basin or Valley, or as Salton Sink. This depression has often received the discharge of Colorado River, which at least once and almost certainly twice, perhaps oftener, has produced an inland sea more than 300 feet deep, 105 miles long and, at the widest point, 35 miles across. The clear-cut beach line of this lake extend from just above Indio, California, to the Mexican boundary and the lake extended about 20 miles farther southward.

The name that we accept for this ancient lake is chosen from three that have been proposed. Though the existence of this lake has been recognized since it was originally described by Blake in 1857, it was first named, as Lake LeConte, by Bailey in 1902. This name has clear priority and commemorates an able pioneer geologist, who made studies in the basin. Through the years this designation has been adopted by several competent geologists, including Gale (1913*a*), Lee, Stone, Gale and others (1915), Boutwell (1933) and Hinds (1943). Blake did not propose the name Lake Cahuilla until 1907, fifty years after the publication of his classic report on the geology of the region. Mendenhall (1909*b*) accepted this name, but mentioned that until Blake's note appeared he had intended to propose the name Blakes Sea. Despite the abortive proposal, the name Blake Sea was adopted by Free (1914*b*), who first detailed the nomenclatorial tangle, and by MacDougal (1914), Grinnell (1926) and Rogers (1939). Others, including Brown (1923), Darton (1933), W. J. Miller (1944), Cockerell (1945, 1946) and R. R. Miller (1946*a*), have followed Blake and Mendenhall in accepting the name Lake Cahuilla. Hanna (1926) altered the spelling to Lake Coahuila.

With few exceptions, students of Lake LeConte (or Lake Cahuilla, or Blake Sea) have regarded it as much younger than the Pluvial lakes of the Great Basin proper. They attribute its formation to a temporary diversion of the Colorado River from the Gulf across its delta into Salton Sink, rather than to the increased precipitation and reduced evaporation of a pluvial period. Several authors, including Mendenhall (1909*b*), Free (1914*b*) and MacDougal (1914, 1917), have considered the probability that the basin filled and desiccated repeatedly—but then reverted to the view that all the observed lake features resulted from a single very recent inflow.

Our observations, around the lake bed and southward across the delta region to its end at San Felipe, Baja California, lead us to believe strongly: (1) that the main stage of Lake LeConte had a prolonged existence ending several thousand years ago, and perhaps, as Cockerell (1946) recently suggested, as ancient as the Pluvial period; (2) that the basin has been predominantly dry since the main stage; (3) that the last complete filling of the depression, to (or nearly to) the outlet level, occurred much more recently and was of very short duration, relatively speaking; (4) that a marine period or stage existed, also rather recently, either when the last complete filling had evaporated to high salinity or, more probably, at some time previous to the last main fill; and finally, (5) that the marine mollusks of this stage invaded the basin with high-tide overflows from the Gulf of California.

MAIN STAGE OF LAKE LECONTE.—Although some lines of evidence (pp. 106–108) confirm the view that a deep lake existed in the Salton Sink only a few centuries ago, other sharply contrasting lines of evidence date the main fill or stage as very much older. The "Ancient Beach Line" bears a striking resemblance in many ways to the uppermost shore features of Lake Bonneville, Lake Lahontan and numerous smaller Pluvial lakes in the Great Basin. In some respects it may be sharper, but this could be accounted for by the very light rainfall of the region and by the lack of frost, or could be attributed to a briefer duration of the lake or to the effects of the very brief and recent lake stage described below.

The rock incisions are not very deep (though not so shallow as some have said), but the rocks are hard and the duration of the lake may have been limited. Since the wave action in Lake LeConte must have been relatively slight, the observed cliff notching probably required many centuries. A report by F. P. Shepard and U. S. Grant, IV (1947) indicates that for several decades there has been almost no appreciable recession of the hard-rock ocean cliffs in southern California.

The 30-inch deposit of alga-formed calcium carbonate on Travertine Rock (Jones, 1914) must have taken a long time to form and it has a very ancient appearance, much like that of the tufa that was formed by Pluvial lakes in Nevada. The great sand bar that connects Travertine Rock and adjacent outliers with the Santa Rosa Mountains must also have required a prolonged construction period. This and many other beach features seem very ancient.

The antiquity of the ancient beach line is also suggested by the apparent changes in its level, though the significance of the data has been questioned and the subject calls for more inquiry. As Kniffen (1932) noted, the Reconnaissance Map of Salton Sink, California (U. S. G. S.) indicates the elevation of the beach above sea-level to vary from 26 feet (or from less than 22 feet at one place in Mexico, where the data are said to be approximate) to 58 feet. In this connection it should be recalled that there has been little alteration of the beach levels of Pluvial lakes in the Great Basin.

The strongest evidence for the great antiquity of the main stage of Lake LeConte is probably furnished by the mollusks that it produced (Blake, 1857, with Appendix III by Gould; Stearns, 1879, 1901; Orcutt, 1890; Kniffen 1932; Cockerell, 1945, with additional references). Though the species were few the individuals were in inestimable millions, much as were the mollusks of Lake Lahontan. By far the most numerous was the tiny *Hydrobia protea,* which is known to have lived contemporaneously with the travertine formation, because, as Jones (1914) and others have noted, shells of this species are locked in the tufa nodules.

Some of the LeConte shells remain near the shoreline, where they lived and died; those that lie over the desert surfaces occur in obvious washes. The unconsolidated shell deposits several feet thick along the Salton Sea shore, near Fish Springs, for example, clearly result from down-washing and beach sorting. The down-washing must have been continuous for millenia, we think, because the shells of the LeConte mullusks occur in sand strips deep down in the alluvial fill of the basin. We found them in fine to coarse bajada alluvium on both sides of the basin in the deepest exposures (8, 10 and 15 feet). Even the fine alluvium that was examined represents lateral inwash rather than a lake deposit, for the strata are crossbedded and are interpolated between streaks of coarser material. Stearns (1879) reported the shells in a clay nodule from near the bottom of a well nearly 50 feet deep.

Still more impressive is the finding of LeConte mollusks in sandy streaks to depths of at least 18 feet in the valley floor, in exposures of the highway cut leading to the New River entrenchment west of El Centro. Except for a few bands that may represent playa deposits, the intermixed and overlying strata are nearly all crossbedded. Obviously the valley fill, so far as here exposed, is basin alluvium, not a lacustrine deposit. Since this is at or near the type-locality of the "Coahuila Silt," we do not concur with Hanna's (1926) indication that this alluvium was "deposited in the freshwaters of ancient Lake Coahuila." Here as elsewhere around the basin the shells appear to represent a redeposit from desert floods. The evidence points strongly against the commonly accepted view that the mollusks lived where the shells are now produced and also points against the opinion of Blake (1914) that they dropped to the bottom to become entombed. Some of the LeConte mollusks may well have lived in deep water or at low lake stages, but if so, we have not seen the strata containing their shells.

Lake LeConte probably produced lacustrine deposits, but if so, they must be buried beneath Salton Sea or, more likely, beneath the age-long bajada and bottom deposits. Several authors, following Blake (1857), have regarded the superficial deposits over the sides and floor of the basin as lacustrine and Jenkins so mapped the entire lake bed on his 1938 Geologic Map of California. In line with our interpretation, however, other authors, including Free (1914*b*) and Brown (1923), have regarded these deposits, largely or entirely, as ordinary desert basin alluvium. Still others, including Mendenhall (1909*b*) and Strahorn, Watson, *et. al.* (1922), have regarded these deposits as a composite of the two types.

Another evidence of antiquity is the failure to find artifacts or other signs of human habitation in littoral formations that are definitely attributable to the main stage of Lake LeConte or to the following prolonged period, during which the sides and bottom of the lake basin were being covered by lateral inwash. Such artifacts were sought for in vain within the bar material along the base of the Santa Rosa mountains opposite Travertine Rock and in several exposures of the alluvium below the ancient beach line.

It seems clear that the main stage of Lake LeConte was much older than is commonly thought. Cockerell's (1946) suggestion that it may have been of Pluvial age, receives some support not only from the indications of great antiquity just recited, but also from evidence that the flow of the Colorado River was greatly increased at that time. In place of now generally dry washes it received great tributaries, notably the Pluvial White and Carpenter rivers (pp. 96–102). Such increased flow might have accelerated delta formation and allowed a prolonged diversion into Salton Sink, sufficient to fill and overflow the basin. During Pluvial times, however, it is postulated that the sea-level was reduced. This would have led to an entrenchment of the river through the delta. For this reason we suspect that the main stage was Interglacial, perhaps between the two divisions of the Wisconsin, or early Postglacial.

Whether what we call the main stage of Lake LeConte involved substages of varying levels or perhaps two or more wholly separate stages is not clear. Each main filling would probably have risen to about the same height, that of the delta top, and might have eradicated the older shore features. Successive fillings would probably have led to distinguishably separate travertine deposits, but on this point the evidence, unfortunately, is conflicting. Jones (1914) bespoke the uniformity of the deposit, whereas MacDougal (1917) claimed to have found proof of several periods of deposition. With reservations, Sykes (1937) agreed with MacDougal. In general the layer where exposed in section seems to be homogeneous, but in places it is smoothly cracked near the middle.

The spectacular variability (Stearns, 1901) of the shell of the superabundant Lake LeConte snail *Hydrobia protea* and the less extreme variation of *Physa humerosa* can be explained most plausibly on the theory that populations of these gastropods lived separately under different conditions. A prolonged lake stage broken up into substages might have provided the environmental background for the development of such variations. A large, continuously interbreeding population of relatively short duration, such as would have existed in a single, brief high lake stage, would not be excepted to produce the observed variability (Huxley, 1943). It is true that the distinctive variations occur together in single deposits—to the amazement and confusion of conchologists—but in our interpretation the present accumulations represent the redeposit of shells that have washed in from various places and from different times. An alternative theory is that the variations represent distinct forms, the products of explosive ecotypic evolution, comparable to that of cichlid fishes in African lakes.

LAST HIGH STAGE OF LAKE LECONTE.—Much of the often stressed evidence for the recency of Lake LeConte seems to us to be valid, but, in view of the contradictory considerations discussed above, we interpret that evidence as pertaining to a brief lake stage that followed the main stage after an entirely or chiefly dry period of prolonged duration.

An impressive part of this evidence stems from or confirms the Cahuilla Indian legend recited by Blake (1857), to the effect that the beach line represents an old lake on which the ancestors of the Cahuillas lived. Going into detail, the legend stated that a rise in lake level once destroyed the lakeside villages; that the lake abounded in fish, and that it dried up, little by little. Mendenhall (1909) added that the time since the lake vanished was said to be the life-span of four or five old men. It is true that Russell (1885) reported legends of great waters in the Lahontan area, where the Pluvial lake was presumably too remote for the perpetuation of a true account. It is also recognized that Indian legends are notoriously unreliable. The one that refers to the last high stage of Lake LeConte, however, is not only detailed, but is also very plausible and is supported by a large amount of concrete evidence.

In confirmation of the legend, relatively recent Indian occupation sites, with piles of charred fish bones, almost continuously line the ancient beach (Rogers, in Jaeger, 1933 and 1938). Some of the stones about the house sites are coated with travertine, indicating a rapid rise in lake level. A record of the "little by little" recession of the lake is seen in the numerous strand lines, marked as much by files of desert shrubs as by changes in gradient. These lines are scarcely distinguishable from the recessional levels of Salton Sea, formed since 1907 at lower elevations in the same basin (Free, 1914*b*; MacDougal, 1914; Sykes, 1937). It seems clear, however, that the large bars at Travertine Rock, on which these recessional lines are so prominent, were formed during the earlier, main stage of Lake LeConte, much too long ago to have preserved on its sandy slopes the slight notching of a receding shore line.

Ichthyological evidence again checks with that derived from other sources. In line with the Indian legend and with expectation from physiographic data we have just found that large fish of Colorado River types abounded at a rather recent time in Lake LeConte. Near the thinning top of the tufa coating on Travertine Rock we have found in the crevices beneath and between the boulders large quantities of fish bones. Although only one charred piece was found these fragments obviously constitute a kitchen midden. Most of the bones are taken to be the remains of half-grown to adult bonytails, *Gila robusta* (a large cyprinid characteristic of the Colorado River fauna). A few pharyngeal arches seem to have come from another large Colorado River cyprinid, the "white salmon," *Ptychocheilus lucius*. Two pharyngeals represent the sucker family, Catostomidae, that is also common in the Colorado. Proof of the recency of this bone deposit is seen in the dried flesh that clings to a few of the fragments. When heated in a crucible, this flesh gave the expected reaction of organic matter.

The recency of the desiccation of the last high stage of Lake LeConte is further indicated by the very slight, at most racial differentiation of the well-separated relict populations of the "desert minnow" (as indicated by preliminary studies). Until the last few decades, during which the springs have been tampered with and the Colorado River was caused to flood the sink, this species, *Cyprinodon macularius,* maintained several residual colonies in isolated springs above and below the old beach line (Miller, 1943*a*). Until others were introduced with the inflow flood of 1905–1907, this species was the only one known from the Salton basin. It has now been eliminated from most of the springs, through their desiccation or through their flooding by Salton Sea, but it has become abundant in the now saline lake. It may have been the small fish for which Fish Creek and Fish Creek Mountains were named, but we can not be sure, as no specimens were preserved and the fish seem to have been wiped out, reputedly by a cloudburst in 1916. It seems plausible to assume that the native fish faunas of the other streams in the drainage basin, such as the upper permanent parts of Carrizo Creek, San Felipe Creek, Palm Canyon and Whitewater River, were similarly eliminated by prehistoric floods. That some of these creeks have remained habitable by fish, even during recent drought years, is proved by the establishment of introduced species—for instance, of *Gambusia affinis affinis* and *Lepomis cyanellus* in Carrizo Creek and, as an experiment, of the Mohave chub, *Siphateles mohavensis*, in the Sentenac Canyon section of San Felipe Creek.

We conclude that there is strong biological as well as physiographic evidence for a recent refilling of Lake LeConte to approximately the ancient high level, probably the overflow level. A rather precise timing appears possible from the archeological approach. Referring to this lake stage, which, however, he failed to distinguish from the ancient main stage, Rogers (1939: 4) estimated the time of the lake's "inception around 1000 *A. D.,* and its extinction between 1400 and 1500 *A. D.* with a duration not in excess of 450 years." On the basis of the dating of pottery types Malcolm Farmer (personal communication) dates the last lake stage, approximately, as from 800 to 1450 A. D., and states that the presence of pottery in the lakeside habitation sites precludes any much earlier dating. How precise such datings may be remains to be seen. They are in rough agreement with the tentative estimates of Mendenhall (1909*b*) and some other geologists and are in harmony with the order of time indicated by many other lines of evidence. They are in conflict, however, with the indications that the main stage of Lake LeConte was much older. They are also out of agreement with MacDougal's (1917) estimate that the origin of Lake LeConte was only 300 or 400 years ago.

Since the last high stage was so brief that it left unimpressive physiographic evidence of its separate existence, there is no assurance that similar fillings did not occur during the prolonged interval that had elapsed since the main, ancient stage. The lack or paucity of lacustrine deposits at elevations higher than about 200 feet below sea level (p. 105) indicates that such fillings were few or brief, or that they, like the floodings of historic time, covered only the lower parts of the basin. Particularly impressive in this connection is the evidence that delta deposits did not extend far into the lake bed. Along the New River near El Centro, to depths of at least 20 feet, the valley fill consists of lateral inwash rather than of delta (or lacustrine) deposits (p. 105). In fact the delta seems to be a half-fan, with a steep northern gradient (Kniffen, 1932).

Two lake fillings during the period of human occupation were definitely postulated by MacDougal (1917) and were more reservedly suggested by Sykes (1937), on the basis of what they thought to be renewed travertine deposits over flooded pictographs on Travertine Rock. Such redeposit might have occurred during the lake rise that flooded the Indian settlements (p. 107). On examining many of these carvings in the travertine, however, we observed that the marl nodules were truncated in even the most obscure scratches, indicating no renewal of the tufa formation. A further study seems needed.

The Marine Stage of Lake LeConte.—Much has been written about the beach line representing a former northward extension of the Gulf of California. This was, indeed, a natural supposition, since the Salton Sink is below the sea and since the Lake LeConte shoreline averages only about 40 feet above mean sea-level and in most places is higher than the lowest part of the delta crest. Although indications of an early marine stage may be buried deep beneath the basin alluvium, as Mendenhall (1909*b*) and others have suggested, it can be stated with considerable confidence that the Gulf did not extend into the Salton Sink within Pleistocene time, therefore probably not within the history of the Colorado River as a whole (p. 94). The marine fossils in the basin are all regarded as Miocene or Pliocene (Hanna, 1926) and probably antedate the present physiographic structure. Despite the fact that the mollusks attributable to the main stage of Lake LeConte are fresh-water forms, it has commonly been held, since the first proposal of the theory by Blake (1857), that the lake was formed by the growth of the delta across the upper end of the Gulf and that thereafter the salt water in the basin was gradually replaced by inflowing fresh water from the Colorado River. Several lines of evidence, presented first by Free (1914*b*) and more recently by Buwalda and Stanton (1930) indicate, contrary to the view of Brown (1922, 1923) and others, that the Salton basin was depressed contemporaneously with the formation of the delta.

Although both the main stage of Lake LeConte and the last high stage were clearly fresh-water, there obviously was a marine stage or period, generally overlooked. On the surface of Salton Sink, between elevations of approximately 150 to 250 feet below sea-level, there have been found many shells of marine and estuarine mollusks. (In this study of the mollusks we have been greatly aided by Joshua L. Baily, Jr., and by S. Stillman Berry.) There are several literature records of the lamellibranch genera "*Gnathodon*" (=*Rangia*) and *Tagelus* and of the gastropod genus *Acteocina* (Cockerell, 1945, and authorities there cited). The single shell of *Ocinebra* (=*Tritonalia*) *poulsoni* mentioned by Stearns (1901) may have been brought in by man. In an old embayment north of Pope, a railroad station on the east side of the basin, we have just found in abundance another marine clam, genus *Chione*. Large accumulations of paired valves and very small specimens of this genus indicate to us and to malacologist S. Stillman Berry, who has examined the site with us, a natural occurrence at approximately this location.

This as well as other evidence refutes and obviates the various roundabout theories that have been proposed to account for the presence of these marine mollusks in a body of water that has generally been interpreted as fresh. It is obvious that the paired valves and minute young clams were not carried by man, or by flood flow from the Gulf, to this distant bay of Lake LeConte. We certainly cannot subscribe to Cockerell's (1945) belief that "these few marine shells cannot be taken to indicate marine conditions"; much less to his suggestion that "they may have been blown by the wind from the shores of the Gulf or they may have come in the excrement of birds" (Cockerell later, in 1946, modified his views, by postulating that the marine gastropod *Acteocina* lived in the lake toward the end of its existence). There is no evidence, known to us, to support the view (heard verbally) that the clam shells were washed out of older fossil beds, to be redeposited on the floor of the valley below. The work of Hanna (1926), of Buwalda and Stanton (1930) and of others (referred to by Cockerell, 1945) indicates that there was no marine invasion of the area after the laying down of the Miocene or Pliocene beds. Neither the location of the outcrops of those beds nor the composition of their faunas supports this concept of a secondary deposit. Furthermore, the fresh appearance of the shells and their freedom from matrix is irreconcilable with that idea. Orcutt's (1890) confusion of part of these late Quaternary shells with the Miocene or Pliocene fauna may be passed over.

All the marine mollusks mentioned above probably lived in the same stage of the lake, though there is evidence of considerable ecological segregation. At present, to the confusion of some conchologists, their shells are mixed with those of Lake LeConte fresh-water species. Such mixture, however, is attributable to the down-washing of the older fresh-water species (p. 105).

The occurrence of the marine shells throughout the basin only at lower elevations suggests that the mollusks lived in a saline body of water intermediate in level between that of the high stages of Lake LeConte and that of Salton Sea at present. In the ancient bay mentioned above, *Chione* and *Rangia*, though common on the plain, rather abruptly disappear on the slope at elevations above –150 feet; that is, at about 200 feet below the main LeConte beach line. Had these clams lived in a shut-off arm of the Gulf before the freshening of Lake LeConte, in agreement with the now generally discarded belief of Blake (1857). Orcutt (1890) and Grinnell (1926), or had they existed in the saline remnant of the main stage, most if not all of their shells would probably have been buried deep in the subsequently deposited alluvium, where none have been seen. Had they lived under either situation the paired valves of *Chione* would certainly not have persisted in local abundance in the surface mud where we found them. It seems probable that these mollusks lived in the saline water which, on further evaporation, produced the superficial and therefore relatively recent salt bed (Bailey, 1902; Mendenhall, 1909*b*; Blake, 1914; Free, 1914*b*; Ross, 1914), now flooded in the lowest part of the sink.

It is possible that the marine mollusks populated the saline remnant of the last high stage of Lake LeConte as the result of fortuitous means of dispersal, but it seems much more plausible to assume that they entered the basin during a partial flooding by very high Gulf tides over the low trough along the western edge of the delta. Such flooding would have been very recent, geologically speaking, but could have occurred before, during or after the time when the last high stage had been reduced to a salt lake. Or, the inflooding may have occurred toward the close of a previous ephemeral high stage, though almost certainly long after the main stage. In view of the changes in sea-level involved, we favor the idea that the marine stage preceded the last high fresh-water stage.

The theory of inflooding would not necessarily be invalidated by the acceptance of the (to us somewhat dubious) claim of Ross (1914), Buwalda and Stanton (1930) and others that the salt beds resulted from the evaporation of Colorado River rather than of Gulf water. Only a small inflow of Gulf water could have seeded the saline lake with mollusks from the head of the Gulf.

The theory of Gulf inflow, which we favor, finds support from indications of relatively recent changes in Gulf level. Such indications were observed by Hubbs, during April, 1947, in the upper part of the Gulf, particularly about San Felipe. At the last main period of cliff and canyon erosion, probably toward the end of the Pleistocene, the sea stood as much as 30 feet above its present level. The period of erosion continued as the sea fell to (or had risen from) below its present height, for some of the canyon cuts extend from the 30 foot notch to below sea-level. During the low sea-level stage (Wisconsin Glacial time?), such canyons were choked with coarse alluvium and an alluvial apron formed along the coast. The top of this apron forms the most conspicuous coastal plain level and is presumably chiefly what Kniffen (1932) saw in the San Felipe region. This sequence of erosion, followed by alluviation, is observable along the western coast of Baja California and of southern California, where these processes appear to have been the last Quaternary events preceding the current cycles of erosion. About San Felipe there is definite evidence of a subsequent temporary rise of the Gulf to about 15 or 20 feet above present level. The evidence is the truncation of a soft canyon fill on Cerro de San Felipe, the planation of parts of the coastal apron, and the coating of these new sea-levels with coquina. A strip of this coquina extends as a veneer onto the exposed cliff face below the 30-foot notch, indicating the recency of this 15–20 foot level. The relative recency of this elevation is further indicated by the finding of many midden shells and pieces of charcoal in an ancient beach that was formed, at about 5 feet present elevation, before or during the rise.

Indications of a recent temporary rise in Gulf level extend from San Felipe to Cerro Prieto. The fresh marginal truncation of the alluvial apron, causing it to look like a long row of mine dumps, obviously represents marine erosion at a recent higher-than-present Gulf level. This striking physiographic feature is to be seen here and there along the Sierra Pintada and almost continously along the Sierra Mayor and the Sierra Cocopa to the end of the recent Gulf extension, just south of Cerro Prieto. Kniffen (1932) misinterpreted this truncated apron as evidence for a rise in land level and erred in regarding it as a direct continuation of the Lake LeConte shore-line. If our interpretations are correct it is a much more recent feature and the rough correspondence in elevation is coincidental. Further evidence for a rise in the water level at the head of the Gulf is the finding of some marine clam shells and in one place of many shells of an intertidal gastropod, *Cerithidea albonodosa,* mixed with fresh-water snails (*Helisoma tenue*) above present tide level on the surface of the flat between the lower Rio Hardy and the truncated alluvial apron.

Disregarding a subsequent fall in sea-level followed by a rise to a few feet above the present (to leave slight cliff notches and stranded lagoons), we may look to the 15–20 foot rise as the one that could have allowed 30-foot tides to overtop the barrier at Volcano Lake. This lake on the delta crest is indicated on the Reconnaissance Map of Salton Sink, California (U. S. G. S.) to be only 24 feet above mean sea-level. In fact the most plausible explanation for the formation of the New River–Volcano Lake–Rio Hardy trough (Kniffen, 1932) seems to be that it was cut by high-tide currents flowing into the Salton basin. The down-cutting presumably continued for a time as the sea-level fell. Had the crest of this trough been at present elevation when the Gulf temporarily rose to 15 or 20 feet above present level, even the ordinarily high tides would have completely filled the Salton Sink and would have left mollusks of many species at high levels.

In line with this physiographic evidence, the following facts regarding the marine mollusks of the Salton Sink indicate that they were introduced by relatively recent high-tide flooding:

(1) they occur only at the surface, so far as known;
(2) they are confined to the lower parts of the old lake bed;
(3) they do not appear to be old fossils;
(4) they are intertidal mud-flat forms;
(5) they, or close relatives, presumably occur in appropriate habitats in the upper Gulf (this last point calls urgently for more detailed study);
(6) they are warm-water types.

Presumably fishes and many other animals entered the marine stage of Lake LeConte along with the mollusks. As yet, however, none of their remains have been found, except, perhaps, the several genera of Foraminifera that Cockerell (1945) mentioned as having been dredged from Salton Sea.

The failure of marine mollusks to populate Salton Sea, now with a salt content not unlike that of the ocean (recent determinations by Martin W. Johnson show a salinity range from 27.81 to 28.40 parts per thousand), is an argument against the idea that they were fortuitously introduced in the past. The barnacles that appeared in Salton Sea during the war and rapidly multiplied to stupendous quantities (Hilton, 1945; Cockerell, 1945) are traced to introduction on the floats of Navy seaplanes or on boats or buoys that were hauled in from the sea coast. The one polychaete worm (a *Neanthes*), which has shown a similar though less spectacular increase, was probably established as a result of efforts by the California Division of Fish and Game in 1929–

1930 to introduce striped bass, *Roccus saxatilis,* along with worms and other food organisms for the fish (Martin W. Johnson and Olga Hartman, personal communications). The "desert minnow," *Cyprinodon macularius,* of a semimarine genus, spread through Salton Sea from flooded springs and, perhaps, from the incursion of Colorado River water in 1905–07. The two other fishes at present in the Sea, the abundant mullet, *Mugil cephalus,* and the rare tenpounder, *Elops affinis,* although chiefly marine, clearly arrived by river route (Coleman, 1929; Dill and Woodhull, 1942; Dill, 1944). The fresh-water fishes that populated the Sea at first (Evermann, 1916) have become extirpated, or confined to the mouths of the distributary streams. The characteristically marine plankters, plant and animal, that have also appeared (Martin W. Johnson, manuscript in preparation), may well have been introduced accidentally with the barnacles or with the fish and fish food. Or, still more likely, they may have been transported in the bilge water of planes that had been flown in from many points between the South Seas and southern California, for Hilton (1945) reported testimony that such bilge water was often pumped into the Salton Sea.

69*b′*.—LAKE CLARK (and other subsidiary waters).—Several small playas, located in Borego and San Felipe valleys, and the marsh areas behind outlet canyon barriers in San Felipe, Mason and Vallecitos valleys (Brown, 1923), as well as Benson Dry Lake at Ocotillo and several playas farther out on the floor of the Colorado Desert, no doubt contained water, at least intermittently, in Pluvial times. They obviously drained into Lake LeConte, however, and were of little significance.

It is highly improbable, however, that there was any discharge from Clark Valley, to the east of Borego Valley, at 33° 20′ N. Lat., 116° 18′ W. Long. The Indio Quadrangle (U. S. G. S.) gives the elevation of the playa of Clark Dry Lake as 542 feet and that of the outlet pass into Borego Valley as 665 feet. The ancient lake, as represented by the playa and by dunes along the north and east sides, probably did not rise above the 600-foot depressed contour. For this body of water we propose the name, *Pluvial Lake Clark.* No definite terraces are visible. The basin is now almost completely dry and is fishless, but it probably contained water in Postpluvial as well as in Pluvial times, for the valley abounds in evidences of Indian occupation.

69*c*.—LAKE PATTIE.—The second major lake basin that is cut off from the Gulf of California by the delta of the Colorado River was named the Pattie Basin by MacDougal (1907). It lies in northeastern Baja California south of the Salton Sink, from which it is separated on the north by a rather low divide and on the east by the northern part of the Cocopa Range. On the west it is flanked by the rugged Sierra Juarez, of the Peninsula Range. The only opening into the Pattie Basin is at the southeastern end, where flood waters enter from the Rio Hardy, a distributary of the Colorado River. Historical records indicate that a lake occupied the basin six times between 1884 and 1928 (Kniffen, 1932). The basin floor was dry at the time of our visit in June, 1939. The ephemeral Recent lake is known as Laguna Maquata (Macuata) or Laguna Salada. For the ancient lake that seems to be represented by the highest of the strand lines we propose the name *Lake Pattie,* to commemorate James Ohio Pattie, the first American explorer to reach the head of the Gulf of California by overland route. It seems probable that a lake occupied the basin in Pluvial times, but there seems to be no critical evidence as to its antiquity. We suspect that the basin was flooded by the Gulf during the rise in sea-level discussed above, for the rim lies only a few feet above high tide.

Pattie Basin is without exterior discharge and the few streams that arise on the eastern escarpment of the Sierra Juarez sink immediately into the desert alluvium as they debouch from the mountains. None of these streams is known to contain fish life, but they have not been thoroughly explored. Like the Salton Sink, the Pattie Basin is known to have supported the one fish genus *Cyprinodon,* apart from fish intermittently brought in by Colorado River waters. A population of *Cyprinodon macularius* occurs in a pool known as Pozo del Tule, located along the northwestern edge of Laguna Salada (Miller, 1943*a*: pl. 1, figs. 3–4). A dwarf form of the genus was described by Jordan and Richardson (1907) as *Lucania browni.* It was taken from a very hot spring (Sykes, 1937) about midway along the east side of the basin, but has not been re-collected. Great numbers of fish are reported to have occurred in the lake after each filling, but these of course died off each time as the lake dried up (Kniffen, 1932; Sykes, 1937). After one of the fillings Orcutt (1890, 1891) found the dead fish to be mullets (*Mugil cephalus*). Thus the fish faunas of the Pattie and LeConte basins are as similar as their hydrographic relations.

69*d*–70*d*.—**Disrupted Rivers and Lakes on East Side of Colorado River**

Throughout vast areas in the middle and lower parts of the Colorado basin, in both the Basin-and-Range and the Colorado Plateau provinces, the Colorado receives tributaries only when flood waters rush down the usually dry arroyos (Lee, 1908*a*; Darton, 1910; Free, 1914*a,* Gregory, 1916; Schwennesen, 1917; Bryan, 1922, 1925; Huntington, 1925; Carpenter and Bransford, 1926; Andrews, 1937). Permanent streams and springs are rather sparingly scattered through this area. Those that have been examined by ichthyologists are either fishless, or have species that show definite relationship with those of the more permanent waters of the Colorado system. A considerable number of the isolated populations have become differentiated into distinct subspecies and species. One drainage, the Sonoyta River, is not now a part of the Colorado basin, butit probably was during Pluvial time.

69*d*.—Sonoyta River.—Along the northwestern boundary of the state of Sonora, Mexico, lies the drainage of the Sonoyta River (Bryan, 1925), which may be considered a disrupted segment of the Colorado River system. This desert stream is believed to have discharged formerly into the Gulf of California near the mouth of the Colorado, prior to the time when its course was diverted southward by the great Pleistocene Pinacate lava flows (Ives, 1936, 1942). At present the stream normally sinks into the desert sands near the eastern border of the lava. The fish evidence is in agreement with the reported hydrographic history: the two species known from this drainage (Snyder, 1915; Miller, 1943*a*, pl. 2, figs. 3–4), a minnow, *Agosia chrysogaster,* and a cyprinodont, *Cyprinodon macularius,* are widely distributed in the lower Colorado River system and obviously reached Sonoyta River at a time when this stream was tributary to the Colorado, perhaps when the coastal level was relatively higher so that Colorado River extended farther south. We have not studied specimens of the minnow in detail. It was wrongly referred by Lumholz (1912: 174–175) to "algansea tincella," a species of the distant Valley of Mexico. The cyprinodont on analysis has proved to be a distinct subspecies. This moderate amount of evolution is in harmony with the physiographic evidence of the rather recent isolation of Sonoyta River.

70.—RED LAKE.—The rather large Hualpai Basin in northwestern Arizona, containing the ephemeral Red Lake (map 1, no. 70), is one of the few strictly enclosed basins in this region (Lee, 1908; Darton, 1910; Free, 1914*a*). On cursory examination, Hualpai Basin seemed much too dry for fish life, and no trace of fish was found or reported in the one tributary canyon (Truxton Canyon) that carries any noteworthy amount of permanent water. No clear evidences of a Pluvial lake have been reported, though a playa 6 miles in diameter and a drainage basin 75 miles long strongly suggest that Pluvial Red Lake was more or less permanent.

70*a*.—SAN SIMON VALLEY.—This valley, tributary in flood to Gila River in southeastern Arizona, contains deep lake deposits referred to the Quaternary (Schwennesen, 1917), but, so far as known, no evidence of a Pluvial lake. The soils and waters of San Simon Valley were also described by Carpenter and Bransford (1926).

70*b*.—MORMON LAKE.—Mormon Lake, near Flagstaff, Arizona, is an isolated body of water. Clarence M. Tarzwell, who examined this lake for the U. S. Bureau of Fisheries, found in it only introduced species. Other lakes and pools, largely ephemeral, exist in the same region, and still others occur, sparingly, elsewhere in the Colorado system. At least some of them have been thought probably to represent ancient lakes (Gilbert, 1875*b*). Meinzer (1922), Bryan (1922) and other recent authorities, however, do not believe that the Pluvial period climate was humid enough in this region to have produced many permanent lakes.

The upper portions of the Colorado system include some headwaters that are isolated except in flood. No local differentiation there has been reported, however, except for one subspecies, *Rhinichthys osculus thermalis* (Hubbs and Kuhne, 1937). This dace is confined to Kendall Warm Spring, Wyoming, adjacent to Green River but isolated from it by falls.

70*c*.—RED DESERT BASIN.—Straddling the Continental Divide in Wyoming is a large, very arid basin of interior drainage, which, from the lay of the land, Free (1914*a*) perhaps rightly regarded as a rather recently disrupted part of the Colorado River system. The intermittent streams in at least the western part of the basin, including Bear Creek which arises in permanent springs, lead to depressed sinks (Nace, 1939), and we doubt that any surface water discharged from the basin in either Recent or Pluvial time. Our own limited examination of this rather inaccessible basin and a more thorough exploration made at our behest by Leonard P. Schultz have both failed to yield any fish specimens. This is unfortunate, for the Colorado River fauna is totally unlike that of the Platte River system just to the north, and almost any native fish would provide a clear indication of the past drainage relation.

70*d*.—LAKE ANIMAS.—In the southern part of the now arid Grant County, New Mexico, south of the Gila River system, beaches, terraces, and embankments indicate the former existence of Pluvial lakes (Huntington, 1914; Schwennesen, 1918; Meinzer, 1922; Jones, 1940). The westernmost of these, lying in Animas Valley, was described and named Lake Animas by Schwennesen (1918: 86, pl. 1). It appears to have had 2 stages. During the lower stage, presumably Pluvial, a lake about 15 miles long and 40 feet deep existed in Lower Animas Valley. In Upper Animas Valley, to the south, the Recent elevations of shore features lie 190 feet higher than the divide separating the Animas and Gila drainages. However, no lake could have existed in this part of the valley under present topographic conditions. The elevated position of the lake remnants may be attributed, in part at least, to subsequent orographic changes. Until further study is made, it may be assumed that an earlier, larger lake (Prepluvial?) covered both Upper and Lower Animas valleys and was connected with a large lake in the Gila Valley. However, no evidence of such a lake in that valley has been reported. Dorton (1933: 168) claimed that the playas west of Lordsburg, to which Animas "River" is tributary, occasionally, discharge into Gila River.

DISRUPTED PARTS OF THE YAQUI RIVER SYSTEM

Basins of interior drainage in North America are by no means confined to the Great Basin and to the disrupted parts of the adjacent Columbia, Sacramento and Colorado systems. Others occur in the United States in disrupted portions of the Yaqui and Rio Grande systems and on the Great Plains. Much of north-central Mexico is also a land of interior drainages, and independent systems occur still farther south, as in Yucatan and Guatemala. For completeness and for comparison we briefly mention these drainages and their fish faunas, though we do not include them in our tally of interior drainages (Table I) nor on the map we have prepared of Pluvial waters.

70*e*.—**Lake Cochise**

Sulphur Spring Basin in southeastern Arizona is cut off by low divides from both the Yaqui River system to the south and the Gila River drainage to the north. It contained Pluvial Lake Cochise, described and mapped by Meinzer and Kelton (1913: 34, pl. 1; further discussed by Darton, 1933: 156–157, sheet 21). It was called Sulphur Spring Lake by Jones (1940), who failed to appreciate that Meinzer (1922) used "Sulphur Spring" merely as the name of the valley or basin. Free (1914*a*: 51) claimed that the basin was tributary to Gila River but Meinzer and Kelton determined that the lake had no outlet. A lake, perhaps of "earlier pluvial" age and similar to that which occurred in San Simon Valley (p. 114), lay in the same area as Lake Cochise and was discussed by Meinzer and Kelton (1913: 57–59; 74–75). This body was presumably a part of the Colorado River system. An inadequate sample of minnows of the genus *Agosia* from the Cochise basin fails to indicate the drainage history. Canyons immediately to the south of the basin contain Yaqui River fishes.

70*f*.—**Lake Cloverdale**

San Luis Valley lies just south of Pluvial Lake Animas (70*d*), along the New Mexico-Mexico border. It occupies an interior basin separated from that of Animas Valley by a low divide about 9 miles north of the international boundary and from the Yaqui River system by a low divide about 4 miles south of that boundary. An exceptionally well-formed beach ridge, 15 to 70 feet high, indicates that a lake once occupied the depression. This Pluvial body was named Lake Cloverdale by Huntington (1914: 70) and was further described and mapped by Schwennesen (1918: 100–104, pl. 1). It was elliptical in outline, about 7 miles long and 5 miles wide, and its major tributary, Cloverdale Creek, still maintains a small but permanent flow in its upper course. No outlet has been described for the ancient lake and it probably had no Pluvial discharge. Free (1914*a*: 51) claimed that it was tributary to the Gila River. Pending further study, we regard the lake as a disrupted portion of the Yaqui River although a Prepluvial discharge might have occurred into both the Yaqui and Gila rivers. Unfortunately there is no fish data to indicate which way the discharge went, for Cloverdale Creek is reliably reported to be fishless.

DISRUPTED PARTS OF THE RIO GRANDE SYSTEM

In southern New Mexico and northern Mexico, between and south of the Río Grande and the Gila River headwaters, there are several isolated lakes and streams which represent disrupted segments of the Río Grande system. The fish data, where available, clearly confirm this interpretation.

70g.—**Rio Mimbres**

Just east of the headwater area of Gila River and west of the Río Grande is a basin of interior drainage that still contains a live creek known as Río Mimbres (or Membres). As noted by Free (1914*a*) and mapped by Darton (1933), this stream ends in a flat trough that slopes southward to Laguna de Guzman, one of the bolson lakes on the Sonoran Plateau of northern Mexico. Those lakes, which we will not treat in detail in this paper, support fishes of undoubted Río Grande affinities (Meek, 1904), though they are in part subspecifically and specifically differentiated. The Río Mimbres of New Mexico is not to be confused with a stream of the same name in Mexico, which is tributary to Laguna de Guzman from the south. In the New Mexico stream we collected the Río Grande mountain sucker, *Pantosteus plebeius,* and an endemic *Notropis* that belongs in the *N. lutrensis* group, which is common throughout the Río Grande and the related drainages of northern Mexico.

70*h*.—**Lake Playas**

Playas Valley, east of Animas Valley in Grant County, New Mexico, is the site of an ephemeral lake called Playas Lake which contains water only after rains. There is evidence, however, in the form of terraces, beaches, and dunes, that a much larger body existed here in Pluvial times. This ancient water was described and named Lake Playas by Schwennesen (1918: 108, pl. 1). It formed a long, narrow body about 40 feet deep, but its precise shoreline was not determined by Schwennesen. Darton (1933) recognized the existence of Lake Playas and stated that the lowest point on its rim leads to Lake Hachita, next to be described. According to Free (1914*a*), Lake Playas discharged into the Gila basin. Despite rumors of other fish life, we found only carp in a tank in this now extremely arid valley.

70*i*.—**Lake Hachita**

Hachita Valley, lying just to the east of Playas Valley, is characterized by a well-defined central draw that extends southward and southeastward into Mexico. The traces of an old shoreline and the general features of the broad plain to the eastward in Mexico, briefly mentioned and mapped by Schwennesen (1918: 120, pl. 1), led him to assume ". . . that there existed here one of the lakes so common at a certain period in recent geologic time throughout this area and in adjoining areas in Arizona." We propose to use the name *Pluvial Lake Hachita* for this ancient body, which lay mostly in Mexico. Darton (1933) asserted that the Hachita basin drains into Laguna de Guzman, which was discussed above in connection with Río Mimbres.

70*j*.—**Lake San Augustin**

The San Augustin Plains form a rather large basin which lies just east of the Continental Divide in New Mexico. It was the site of Pluvial Lake San Augustin (Bryan, 1926; Powers, 1933, 1939, 1941). Whether or not this lake attained a Pluvial or an "earlier pluvial" discharge into the Río Grande (as held by Free, 1914*a*) has not been definitely ascertained. Nor has it even been proved that there has been no connection with the Gila River, just to the westward. We have not examined the area, but Dr. Powers tells us that it must be fishless.

70*k*.—**Lake Estancia and Lake Encino**

Estancia and Encino valleys, lying between Río Grande and Pecos River in central New Mexico, were each the site of a Pluvial lake, respectively large and small (Meinzer, 1911*a*, 1922; Free, 1914*a*). Neither of these basins nor any of the other adjacent playa-containing basins of interior drainage has been explored for fish. Antevs (1935) named Pluvial Lake Estancia and discussed its climate and age. We name the other body of water *Pluvial Lake Encino.*

70*l*.—**Lake Otero**

South of the Estancia basin, and likewise intervening between Río Grande and Pecos River, lies the remarkable Tularosa Basin, of interior drainage. This is the site of Pluvial Lake Otero (Tarr, 1891; Herrick, 1904; MacDougal, 1912; Free, 1914*a*; Huntington, 1914; Meinzer and Hare, 1915; Meinzer, 1922; Blair, 1943), also called Lake Tularosa (Jones, 1940). The only fish of this long-isolated basin, a *Cyprinodon,* is confined to Malpais Spring. It shows relationship with forms occurring in the Río Grande and the Red River systems, and was presumably derived by way of an "earlier pluvial" connection with the Río Grande.

70*m*.—**Lakes in Sacramento River–Salt Lakes Basin**

South of the Tularosa depression there lies the Salt Lakes Basin, a large area of interior drainage that finds a sump in the Salt Lakes of Trans-Pecos Texas (Free, 1914*a*: 49; Carter, Beck, Smith, Hawker, Templin, and Reitch, 1928).

The Salt Lakes Basin is probably fishless, according to personal communication from W. Frank Blair, who has carried on biological studies in the region. No one has collected in Sacramento River, a mountain stream of southern New Mexico, nor in another tributary (from the Guadalupe Mountains), both of which discharge into the north end of this valley (Fisher, 1906), but local testimony suggests that these streams as well as the basin proper lack native fish.

70*n*.—**Lakes in San Luis Valley**

The San Luis Valley, in the headwaters of the Río Grande in southern Colorado, is isolated by sand dunes and finds a sump in the alkaline San Luis Lakes (Jordan, 1891*a*; Holmes, 1904; Siebenthal, 1910; Free, 1914*a*; Ramaley, 1942). The theory was expressed long ago, by Stevenson (1875), Endlich (1877) and Whitney (1882), that this basin was occupied by a Pluvial lake. Endlich assumed that the valley contained two ancient lakes which he named Coronado's Lakes, which drained into the Río Grande by the downcutting of the outlets. In the tributary springs and streams of San Luis Lakes, one would expect to find Río Grande fishes; these tributary waters were listed by Jordan as trout streams. The only specimens we have had from the "San Luis Park" are of a species, *Pimephales promelas,* that occurs in the Río Grande. Strangely, however, they are intermediate between the Río Grande–Arkansas River subspecies *confertus* and the northern form, *P. p. promelas.* These fish, from Medano Springs Creek, are probably native, but may have come into the basin from Río Grande *via* Del Norte Canal, to be subsequently dispersed by flood waters.

Ancient lakes are indicated by Stevenson (1875) to have existed in Glacial times in other mountain "parks" in the Río Grande headwaters, as also in the Mississippi drainage farther north.

In addition to the basins, mentioned above, that were already of interior drainage in Pluvial time, there occur through the Río Grande system in New Mexico and Texas a considerable number of sink-hole lakes, and also many headwater springs and creeks (Fisher, 1906, etc.), that are disconnected from the main stream system except during high floods (which, as we have seen, have little effect on faunal connections). Because of their isolation in such headwater springs and creeks, the few fishes of these waters have undergone considerable speciation, for instance in the Big Bend region of Texas (Hubbs, 1940*b*) and in the largely disrupted Pecos River system, in the Trans-Pecos region of Texas (Carter, Beck, Smith, Hawker, Templin, and Reitch, 1928).

ISOLATED DRAINAGES ON THE GREAT PLAINS

In the more arid parts of the Great Plains, from Texas northward, particularly on the Llano Estacado, the High Plains, the Colorado Piedmont, and the Sand Hills Region, there are hundreds of small basins of interior drainage (Free, 1914*a*). As a rule each of these basins comprises dry washes that lead to an ephemeral or saline lake. Few contain native fish life, and no speciation correlated with isolation in these basins has been noted. Some of these basins contained shallow Pluvial lakes, with cool-water mollusks, extinct vertebrates and artifacts (Howard, 1935*a–b*; Antevs, 1935).

An isolated stream in western Kansas, White Woman Creek, contains two fishes, both of which show subspecific relationships with forms of more northern streams. One of these is *Pimephales promelas,* represented locally (as in San Luis Valley, Colorado) by intergrades between the southern and northern subspecies, and the other is the northern black bullhead, *Ameiurus melas melas.* It may be assumed that White Woman Creek was stocked by these subspecies when the creek was connected with the Arkansas River and when the ranges of the subspecies were displaced southward. These assumptions suggest glacial timing, and we have here another bit of evidence pointing toward the correlation of the Pluvial and late Glacial periods—even as far east as the Great Plains.

ISOLATED DRAINAGES IN MEXICO AND GUATEMALA

We have already mentioned that the bolsons of the Sonoran Plateau of Mexico have faunas related to that of the Río Grande. Among the fishes of these waters, there are some endemic species and subspecies and one endemic genus, the cyprinid *Stypodon.* The considerably disrupted Río Lerma system at the southern end of the Plateau has a very distinctive and much localized fish fauna. These relations were treated by Meek (1904) and are receiving further inquiry. Isolation and speciation in certain small interior drainages in San Luis Potosí have recently been noted in the cyprinodont genus *Xenoophorus* (Hubbs and Turner, 1939). The cenotes and caves of Yucatan provide further examples of the speciation of fresh-water fishes correlated with the isolation of the waters they inhabit (Hubbs, 1936, 1938). Among the isolated waters in Guatemala the most outstanding is Laguna de Petén (a very large compound limestone sink lake), where again isolation has resulted in considerable speciation (this lake was studied by the senior author in 1935). Wherever we explore separated drainage systems and the fish faunas they contain, we find correlations between isolation and speciation, and between geology and biology.

CONCLUSIONS

The limited space available in a symposium and the incomplete stage of many of our investigations have forced us to restrict our treatment. The distribution of fish life through the waters of the desert has been presented only in résumé. Theories as to the origin and evolution of fishes in the Great Basin and other areas of interior drainage have been accorded little more than mention (conclusions regarding the speciation of Great Basin fishes have been preliminarily stated in other papers: Hubbs, 1940*a*, 1941*a*, *b;* Miller, 1946*a*, in press). Almost nothing has been said of the distribution in the Basin of animals other than fishes or of plants.

In treating the distribution of fishes valley by valley through the Great Basin, and in other areas of interior drainage, however, we have attempted to show that the ichthyological evidence definitely supplements the geological. In many respects and for many regions the data from the two fields stand in mutual support. The Pleistocene history of the land-forms and of the water systems of the Intermountain region, as elucidated by physiographers, gives ichthyologists a wealth of data on which to base conclusions regarding the history and speciation of fishes in the area. The fish workers in turn often provide confirmation for the interpretations of the geologists, or find distributional or speciational situations that suggest alternative explanations of the hydrographic history.

As yet we may regard as authentic and respectably complete only the general outline of the latest (Pluvial and Postpluvial) periods in the history of the Great Basin and its life. Before the picture is well filled in, specialists in every pertinent field will need to complete researches surpassing those of the past, in the intensive as well as the extensive approach.

In order to provide biologists with what they need, as well as to develop their own field, geologists should extend their field studies into every one of the many basins of interior drainage. Much can be contributed by conducting researches in greater detail and in a more penetrating and critical way—for instance by estimating the age in years of some chapters in the late geological history, through a study of the varved deposits produced during that period. Many should follow Blackwelder's steps in carrying backward the recent history, despite the fact that most of the records of the early ice and lake stages have been erased. The hydrographic history needs to be dated more accurately, and should be correlated more often and more definitely with montane glaciation, and then, somewhere and somehow, we may hope, the mountain glaciers should be correlated with continental glaciation. Accurate topographic mapping is a particular desideratum.

On the biological side specialists in every group need to think in terms of the origins and the histories of the forms of life occurring in the Great Basin. They then need to follow up their thoughts with concrete research rather than with the type of speculation that has been too rife. In particular they should seek constantly to tie in their data with the geological information.

In their classical studies of the Pluvial history of the Great Basin, Russell and Gilbert both made considerable use of biological data, and since then biologists and geologists from time to time have utilized to advantage the data supplied by their colleagues in the other field. We, for example, are eagerly grasping all the geological data that may have an important bearing on our conclusions regarding the systematics, distribution, history and speciation of the desert fishes. We are even attempting, albeit in a sketchy and amateurish way, to interpret by direct observations as well as by biological inference, the past and present hydrography, particularly in regions which have been more or less neglected by the physiographers.

No inconsiderable part of the progress that has been made in elucidating the problems of the Great Basin has come from the joint consideration of biotic and physiographic data. Even greater advances should ensue, when the biological and geological approaches are more definitely integrated. We eagerly look forward to the time when we may join with a glacial geologist to journey, helping hand in helping hand, across the desert mountains and flats of the Great Basin, together attempting to unlock some of the doors that are yet closed to us.

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NOTE — The papers by Hubbs and Miller and by Miller, listed as "in press," were published in 1948 prior to the appearance of this report.

EXPLANATORY REMARKS ON SUMMARY TABLE OF PLUVIAL LAKES AND NOW DISRUPTED STREAM SYSTEMS AND ON MAP OF PLUVIAL LAKES AND STREAMS

The following summary table of lakes and streams covers the Pluvial waters of the Great Basin and the disrupted parts of Pacific drainage rivers from the Columbia to the Yaqui. Included also are disrupted parts of the Rio Grande system in New Mexico, Texas and Colorado. The table is supplemented, on pages 156–165 by a list of references to these waters. Certain isolated waters in Middle America, including the disrupted parts of the Rio Grande system and certain other waters in Mexico, are briefly mentioned in the text but are included on neither the table nor the list of references. The map covers Nevada and parts of adjacent states. It was prepared by the authors and drafted in 1946 by P. L. Mattox of the United States Geological Survey. Some final corrections were made by J. L. McHugh.

Sources for the table and for the map are the publications listed for each lake (pp. 156–165) and numerous separately published maps. Of general application are the State base maps and the topographic maps (quadrangles) of the United States Geological Survey; Plan of Reese River, Nevada (1937) and Plan of Muddy River, Nevada (1937); the Atlas Sheets of the Geographical Exploration West of the 100th Meridian (Wheeler Survey); other old and new maps of the Geological Survey as represented by the complete bound file in the Washington office; the Forest Service maps; and Indian Reservation maps published by the Office of Indian Affairs. For particular states we found useful the General Land Office Map of Nevada (1930), Road Map of Nevada (Automobile Club of Southern California, no date), Resource Map of Utah (Civil Works Administration Project, 1934), Topographic Map of Arizona (University of Arizona, Bureau of Mines, prepared by N. H. Darton, 1933), and the numerous large-scale sectional road maps published by the Oregon Road Commission. Valuable local maps include the Range Map of Charles Sheldon Antelope Range (U. S. Department of the Interior, Grazing Service, 1940–1941), map of White Pine County, Nevada (compiled by F. W. Millard and Son, Ely; rev. ed., 1945) and Map of Clark County, Nevada (C. D. Baker, 1931). For previously very poorly explored areas of southern Nevada we found much help in the quadrangle sheets of the Metropolitan Water District of Southern California, which also cover desert areas of Southern California; a map covering southern Nevada from 36° to 38° N. Lat., and from 114° 30′ to 117° 15′ W. Long. (prepared at the Indian Springs Army Air Field, Las Vegas, Nevada, May 29, 1945); and the Bureau of Reclamation map of Boulder Canyon Project, The Vicinity of Boulder Dam (1940). For most parts of the area covered, the tables and map have been modified or prepared from our own field reconnaissance, principally in the summers of 1934, 1938, 1939, 1942 and 1946. Less extensive field work was done in 1915, 1926, 1935, 1936, 1937, 1940, 1943, and 1945 to 1948.

The map and most of the discussion pertain primarily to the highest lake stages of the Pluvial period. A few of the lakes, however, particularly in southeastern California, were probably of late Prepluvial age. Others may have been Postpluvial. Many of the smaller lakes, particularly in the southern part of the Great Basin, may have been ephemeral even at the height of the Pluvial period. Such qualifications are indicated in the table and in the text, whenever these indefinite lakes are mentioned. The policy has been to include on the map all but the very smallest of the playas that are shown on maps, on the theory (pp.28–29) that nearly all such depressions probably contained at least shallow and semipermanent Pluvial lakes. Only the larger of such lakes, particularly those of the Area of Sterile Basins (map 1, no. 23, lettered units) are designated by number or letter on map 1. Lakes formed by the partial desiccation and fragmentation of the larger Pluvial lakes are not mapped and are usually not indicated in the table nor treated in the text. Only the major, now disrupted Pluvial rivers are numbered and discussed. Other streams, however, are indicated on the map, following the courses of Recent streams and definite dry canyons.

On the other hand, without doubt, many Pluvial waters are not included in Table I or on map 1. Many small mountain lakes were no doubt in existence in Pluvial time, in both glaciated and nonglaciated regions.

An attempt has been made to trace original sources of information on the Pluvial waters. In the list of references (pp. 156–165) an asterisk is affixed to the name of the author who proposed a definite name for the ancient lake or river. Otherwise the name as here listed is either original, or is identical with that of the residual body of water. In some of the summary treatments of Quaternary lakes, particularly those of Young (1914) Jones (1940) and Flint (1947), it is not wholly clear whether the authors were consistently naming the lakes or were frequently giving the names of the valleys or basins in which lie the remnants of the Pluvial waters. We interpret their intention to be the naming of the basins, as Meinzer (1922) often did, with a more explicit column heading, "Name of lake or of containing valley or basin." Authors who have merely copied previous maps of Pleistocene lakes are usually not listed, except wherein they present new data or interpretations, on maps or in the text. The Quaternary lakes as mapped by Russell (1885) are shown on subsequent maps by Gilbert (1890), Meinzer (1917), and Clark and Riddell (1920).

Another map of Great Basin Quaternary lakes was given by Lee, Stone, Gale and others (1915), and reproduced by Boutwell (1933) and Hinds (1943). It is very incomplete, and is not generally referred to under the separate systems.

Meinzer's 1922 map of Pleistocene lakes, consistently referred to with Meinzer's numbers, was the basis of subsequent charts by Antevs (1925), Hay (1927), Jaeger (1933, 1938), Daly (1934), Jones (1940), Nolan (1943) and Flint (1945, 1947).

In the several reproductions of Meinzer's excellent though small-scale map, a number of errors have crept in that might lead to confusion on casual consideration. The most likely source of confusion is the roundish Pleistocene lake shown on Nolan's 1943 map as covering a large area in the Owyhee River system of southeastern Oregon. As explained on page 58, this indicated lake is seemingly a draftman's blot. Hay's 1927 map errs in several details, particularly in showing a minute lake between Fort Rock Lake and Lake Malheur in Oregon, in the separation of the two arms of Alvord Lake in Oregon and Nevada, in the undue thickening of the dashed lines for streams in the Mohave Desert and Death Valley areas, and in the inclusion of a draftsman's slip (a spur in the border line of the Basin and Range Province, in southern California). Jaeger's map (1933 and 1938), obviously traced from Hay's, accentuates some of these slips and introduces others, so that what seem to be lakes are attributable to an imperfect tracing of the stream lines in the Mohave Desert and of the false spur on the border line just referred to. Other "lakes" on Jaeger's map represent the number 1 on Fort Rock Lake, three segments of No. 56 in the Mohave Desert, and the "E" of OREGON on Hay's map.

A very recent modification of Meinzer's map of Great Basin lakes, namely the Western Half of the Glacial Map of North America (Flint, 1945), contributes no new information and is not referred to in the text nor in the lake list on pp.156–165. It was apparently based on Meinzer's map but is defective in several respects. It fails to show 9 of the lakes portrayed by Meinzer, namely lakes Catlow, Juniper, Lebou, Aurora, Garfield, Huntoon, Toiyabe, Butte (=Butte Bay of Lake Franklin) and Thompson. The only lakes included that were not on Meinzer's map are Tulare, Long and Manly. Two lakes are confusingly misplaced—Dixie so as to overlap Lahontan slightly and Gilbert so as to overlie headwaters of Pine Creek. Confusion is introduced by treating islands in the Pluvial lakes in the identical way that the present playa remnants are represented. This recent map and the accompanying table and text by Flint (1947) are referred to only where there is included material not given by Meinzer (1922).

These criticisms of the previous maps of the Pluvial waters of the West are offered in the hope that others who have not followed through the whole literature will not be led to erroneous ideas as to the number and location of these waters.

Under Pluvial Connection (third column of Table I) the hypothesized type of hydrographic connection is indicated by 5 symbols, as follows:

A=Alluvial cone connection, effected by stream wandering from one side of the fan to the other.

C=Stream capture or piracy.

D=Surface discharge.

S=Seepage discharge, through alluvium or lava.

T=Tributary (receiving discharge from basin so designated).

The statement "Basin now fishless," frequently used in the final column of Table I, refers to native fishes only and for some of the less thoroughly explored basins represents our best judgment, based on all available evidence, derived from maps, field examinations and local testimony.

For convenience in cross reference the same numbers are used for the Pluvial waters in text, table, list of references, and map.

Table I.

PLUVIAL LAKES AND NOW DISCONNECTED PLUVIAL RIVERS OF THE GREAT BASIN AND OF THE DISRUPTED PARTS OF THE PACIFIC DRAINAGES, THE PAST CONNECTIONS OF THESE WATERS, AND THE FISH FAUNAL RELATIONSHIPS OF THE RECENT REMNANTS OF THE PLUVIAL WATERS

(See explanation on pp. 145–147)

Pluvial Lake or River	*Valley or Basin*	*Pluvial Connection (Abbreviations Explained on p. 147)*	*Most Plausible "Earlier Pluvial" Connection*	*Relationships of Recent Fish Fauna of Remnant Waters*
Bonneville System (including Snake River above falls)				
1.—Lake Bonneville	Great Salt Lake, Sevier Lake, Great American Desert, etc.	Columbia R., via Snake R. (D)	Same as Pluvial (D)?; L. Lahontan and Colorado R. (C or A)	Uniform throughout; largely distinctive; in part with Columbia, Klamath, Sacramento and Colorado systems
1*a*.—Bear Lake	Bear Lake	L. Bonneville (D)	L. Bonneville (D)	Bonneville system (conclusive)
1*b*.—Little Salt Lake	Parowan Valley	L. Bonneville (D)	L. Bonneville (D)	Bonneville system (conclusive)
1*c*.—Pine Lake	Sage Brush Valley	L. Bonneville (D) (possibly)	L. Bonneville (D)	Basin now fishless
Lahontan System				
2.—Lake Lahontan	Pyramid Lake, Walker Lake, Humboldt River, etc.	Probably none (D); several surrounding basins (C or A)?	First toward SW.?; Klamath Lakes (D)?; surrounding basins (C or A)	Uniform throughout; in part distinctive; in part with Columbia, Klamath, Sacramento, Bonneville and minor systems
Lakes connected with central Lahontan basin				
3.—Lake Newark and Fish Creek	Newark and Little Smoky valleys	L. Lahontan, via S. Fork Humboldt R. (D)	L. Lahontan, via S. Fork Humboldt R. (D)	Lahontan system (evidence weak)
4.—Lake Diamond	Diamond, Kobeh, Monitor and Antelope valleys	L. Lahontan, via S. Fork Humboldt R. (D)	L. Lahontan, via S. Fork Humboldt R. (D)	Lahontan system (evidence moderately conclusive)
5.—Lake Gilbert	Grass Valley	L. Lahontan, via Crescent Valley (D)	L. Lahontan, via Crescent Valley (D)	Lahontan system (presumptive)
6.—Lake probably "earlier pluvial"	Crescent Valley	L. Lahontan, via Humboldt R. (D)	L. Lahontan, via Humboldt R. (D)	Lahontan system (evidence rather conclusive)
7.—Lake probably "earlier pluvial"	Carico Valley	L. Lahontan, via Crescent Valley (D)	L. Lahontan, via Crescent Valley (D)	Basin now fishless
8.—Buffalo Lake	Buffalo Valley	L. Lahontan, via Reese R. (D); not certain	L. Lahontan, via Reese R. (D)	Basin now fishless
9.—Lake lacking or insignificant	Antelope Valley	L. Lahontan, via Reese R. (D)	L. Lahontan, via Reese R. (D)	Basin now fishless
10.—Lake Washoe	Washoe Lakes basin	L. Lahontan (D)	L. Lahontan (D)	Lahontan system (conclusive)
11A.—Lake Tahoe	Lake Tahoe basin	L. Lahontan (D)	L. Lahontan (D)	Lahontan system (conclusive)
11B.—Lake Truckee	In course, Truckee River	L. Lahontan (D)	Non-existent	Lahontan system (conclusive)
12.—Eagle Lake	Eagle Lake basin	L. Lahontan (D, probably, or S)	L. Lahontan (D)	Lahontan system (conclusive)
13.—Horse Lake	Horse Lake basin	L. Lahontan (D)	L. Lahontan (D)	Lahontan system (conclusive)
14.—High Rock Lake	High Rock Lake basin	L. Lahontan (D)	L. Lahontan (D)	Lahontan system (presumptive)
15.—Lake Lemmon	Lemmon Valley	L. Lahontan (D)	L. Lahontan (D)	Basin now fishless

Lakes in enclosed basins surrounded by Lahontan watershed				
16.—Lake Wellington	Basin north of Wellington	None, or possibly L. Lahontan (D)	L. Lahontan, via Walker R. (D)	Basin now fishless
17A.—Lake Laughton	White Lake Valley	Probably none; possibly L. Lahontan (D)	L. Lahontan (D)	Basin now fishless
17B. Lake Fred	Basin east of Fred Mt.	None	L. Lahontan (D) ?	Basin now fishless
18A.—Lake Kumiva	Kumiva (Kumavi) Valley	None	L. Lahontan (D) ?	Basin now fishless
18B.—Granite Springs Lake	Granite Springs Valley	None	L. Lahontan (D) ?	Basin now fishless
Minor Lakes Just South of Lake Lahontan System				
19.—Fish Lake	Fish Lake Valley	Lake Columbus (D)	Lake Lahontan? (indirectly)	Lahontan system (dubious)
20.—Lake Dixie	Humboldt Salt Marsh, Dixie Valley	Probably none	Lake Lahontan	Lahontan system (moderately conclusive)
21.—Lake Labou	Fairview Valley	Lake Dixie (D)?	Lake Dixie (D)	Basin now fishless
22.—Lake Toiyabe	Big Smoky Valley, northern part	Lake Lahontan (C), via Lake Gilbert (problematical); Lake Tonopah (C) ?	Same as Pluvial, or with Lake Tonopah by discharge	Lahontan system (evidence weak)
23.—**Area of Sterile Basins**				
A-G.—Basins adjacent to Lake Lahontan				
A.—Lake Edwards	Edwards Creek basin	Probably none	Dubious	Basin now fishless
B.—Lake Smith	Smith Valley	Probably none	Dubious	Basin now fishless
C. Lake Gabb	Gabbs Valley	None	Probably none	Basin now fishless
D.—Lake Acme	Soda Springs Valley (west)	Possibly L. Lahontan (D)	Lake Lahontan (D) ?	Basin now fishless
D′.—Lake Luning	Soda Springs Valley (east)	L. Rhodes (D)	Lake Lahontan (D) ?	Basin now fishless
D″.—Lake Rhodes	Rhodes Salt Marsh	None	Lake Lahontan (D) ?	Basin now fishless
E.—Lake Garfield	Garfield Flat	None	Probably none	Basin now fishless
F.—Lake Teel	Teels Marsh	None	Probably none	Basin now fishless
G.—Lake Huntoon	Huntoon Valley	None	Probably none	Basin now fishless
H-K.—Basins structurally connected with basins of Lake Toiyabe and Fish Lake				
H.—Lake Monte Cristo	Monte Cristo basin, north of Monte Cristo Mountains	Probably none	Possibly L. Tonopah (D)	Basin now fishless
I. Lake Columbus	Columbus Salt Marsh	Possibly Fish Lake (T)	Fish Lake; perhaps also Lake Lahontan via Lake Rhodes	Basin now fishless
J.—Lake Tonopah	Big Smoky Valley, southern part	Lake Toiyabe (A) ?; Lake Clayton (A) ?	Lake Toiyabe (T) ?	Basin now fishless
K.—Lake Clayton	Silver Springs Marsh, Clayton Valley	Lake Tonopah (A) ?	Lake Tonopah (A) ?	Basin now fishless
L-T.—Basins structurally connected with Death Valley system				
L.—Lake ephemeral?	Ralston Valley	Possibly Stonewall Flat (D)	Stonewall Flat (D)	Basin now fishless

Pluvial Lake or River	*Valley or Basin*	*Pluvial Connection (Abbreviations Explained on p. 147)*	*Most Plausible "Earlier Pluvial" Connection*	*Relationships of Recent Fish Fauna of Remnant Waters*
M.—Lake ephemeral?	Salisbury Wash and Cactus Flat	Possibly Ralston Valley (D)	Ralston Valley (D); Gold Flat (T)	Basin now fishless
N.—Lake ephemeral?	Gold Flat	Probably none	Cactus Flat (D)	Basin now fishless
O.—Lake ephemeral?	Alkali Spring Valley	Probably none	Ralston Valley (D)	Basin now fishless
P.—Lake ephemeral?	Stonewall Flat, NE. part	Possibly Ralston Valley (T); possibly SW. part, same flat	Ralston Valley (T); SW. part of same flat	Basin now fishless
P′.—Lake ephemeral?	Stonewall Flat, SW. part	Possibly basins P and Q (T)	Basins P and Q (T); Sarcobatus Flat (D)	Basin now fishless
Q.—Lake ephemeral?	Basin west of Stonewall Flat	Probably none	Stonewall Flat (T)	Basin now fishless
R.—Lake ephemeral?	Sarcobatus Flat	Probably none	Stonewall Flat (T); Death Valley (D)	Basin now fishless
S.—Lake ephemeral?	Yucca Flat	Probably none	Frenchman Flat (D)	Basin now fishless
T.—Lake ephemeral?	Frenchman Flat	Probably none	Amargosa River (D) ?	Basin now fishless
U-V.—Basins adjacent to Railroad Lake system				
U.—Lake ephemeral?	Willow Creek basin	Probably none	Unknown	Basin now fishless
V.—Lake ephemeral?	Kawich Valley	Probably none	Railroad Lake (D) ?	Basin now fishless
W-Z.—Basins structurally connected with Pluvial White River				
W.—Lake ephemeral?	Penoyer or Sand Spring Valley	Probably none	Desert Valley (D)	Basin now fishless
X.—Lake ephemeral?	Papoose Dry Lake, Emigrant Valley	Perhaps Groom L. (D)	Groom Lake (D)	Basin now fishless
X′.—Lake ephemeral?	Groom Dry Lake, Emigrant Valley	Probably none	Desert Valley (D)	Basin now fishless
Y.—Lake ephemeral?	Desert Valley	Probably none	White River (D)	Basin now fishless
Z.—Lake ephemeral?	Valley just north of Dry Lake Valley	Dry L. Valley (D)?	White R., via Dry L. Valley (D)	Basin now fishless
Z′.—Lake ephemeral?	Dry Lake Valley	Probably none	White R., via California Wash (D)	Basin now fishless
Lakes Between Lahontan, Bonneville and Colorado Systems				
24.—Lake Franklin	Ruby Valley and north part of Butte Valley	Almost certainly none (D); L. Waring (A)?	Clover L. (D)	Steptoe fauna (pp. 51-52)
25.—Lake Gale	Butte Valley, south part	Butte Bay of L. Franklin	Butte Bay of L. Franklin	Steptoe fauna
26.—Clover Lake	Clover and Independence valleys	Probably none	L. Franklin (T); L. Lahontan, via Humboldt R. (D)?	Steptoe fauna
27.—Lake Steptoe	Steptoe Valley, south part	L. Waring (D)	L. Waring (D or conjoined)	Steptoe fauna
28.—Lake Waring	Steptoe Valley, north part[1]	L. Franklin (A)?	Uncertain	Steptoe fauna
29.—Antelope Lake	Tippett basin of Antelope Valley	Probably none	Possibly L. Waring (D) or L. Bonneville (D)	Basin now fishless

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[1] Including main, northern part of Antelope Valley.

30.—Spring Lake	Spring Valley	Probably none	Possibly Carpenter R. (D) or L. Bonneville (D)	Steptoe fauna; also Bonneville or Colorado
31.—Lake probably small and ephemeral	Long Valley	Probably none	L. Franklin?	Basin now fishless
32.—Lake Jake	Jakes Valley	Probably none	Possibly White R.	Basin now fishless
Lakes North of Lahontan System				
33.—Lake Madeline	Madeline Plains and Grasshopper Valley	Sacramento R., via Pit R. (C); L. Lahontan (S)	L. Lahontan (D or S)	Pit R. of Sacramento system (not very conclusive)
34.—Lake Alvord	Alvord Desert and connected basins	None	Possibly with Columbia R. (D)	Fauna distinctive (minnow) or uncertain (trout)
34*a*.—Lake Mann	Mann Lake	None, fide Russell	L. Alvord (D)	Basin now fishless
34*b*.—Juniper Lake	Juniper Lake	None, fide Russell	L. Alvord, via L. Mann	Basin now fishless
35.—Summit Lake	Summit Lake basin	None	Soldier Meadows arm of L. Lahontan (D)	Lahontan system (presumptive) or Alvord basin
35*a*.—Lake Catlow	Catlow Valley	None	Columbia R., via Malheur R. (D)	Uncertain
36.—Guano Lake	Guano Valley	L. Catlow (D); with some doubt	L. Catlow (D)	L. Catlow (moderately conclusive)
37.—Lake Meinzer	Long Valley	None	Probably Warner L., via bay in Coleman Valley (D)	Warner L. (inconclusive)
38.—Lake Surprise	Surprise Valley and Duck Flat	None	L. Warner (D or C) or L. Lahontan (D)	L. Warner and/or Lahontan system
39. Lake Warner	Warner Valley	None (doubt raised by Van Winkle)	Columbia R., via Malheur R. (D)	Uncertain; probably various
40.—Cowhead Lake (not certainly Pluvial)	Cowhead Lake	L. Warner (D)	L. Warner (D)	L. Warner (presumptive) or one of surrounding basins
40*a*.—Alkali Lake	Alkali Lake and adjacent desert	Probably none	L. Chewaucan?	L. Chewaucan (presumptive) or one of other surrounding basins
40*b*. Lake Chewaucan	Summer Lake, Chewaucan Marsh, and Abert Lake	Probably none	One or more of surrounding basins	Uncertain; probably closest with Fort Rock Lake and Alkali Lake faunas, but could be with Klamath Lakes, Goose Lake or Warner Lake fauna
41.—**Klamath River System**				
41*a*.—Klamath Lakes (several)	Klamath River system, upper part	Formerly interior drainage; later with ocean, via Klamath R. (D); Fort Rock L. (C) ?	Probably L. Lahontan first; then probably with Sacramento and Columbia systems	Lahontan system; Columbia R.; Pit R. division of Sacramento system; surrounding lake systems
Caldera Lakes				
41*b*.—Crater Lake	Crater Lake	Lake existent?; certainly no connections	Lake not existent	Lake now fishless
41*c*.—Medicine Lake	Medicine Lake	None	Lake existent?	Lake now fishless
Disrupted Parts of Sacramento River System				
42.—Goose Lake	Goose Lake basin	Sacramento R., via Pit R. (D)	Very early with L. Lahontan??; later with Klamath L.?; finally with Sacramento R.	Upper Sacramento R. (conclusive); Klamath Lakes (probable); Lahontan system (possible)

Pluvial Lake or River	*Valley or Basin*	*Pluvial Connection (Abbreviations Explained on p. 147)*	*Most Plausible "Earlier Pluvial" Connection*	*Relationships of Recent Fish Fauna of Remnant Waters*
42*a*.—Clear Lake	Clear Lake	Sacramento R. (D); Russian R. (D)	Lake not existent?; streams tributary to Russian R.?	Sacramento system (conclusive)
42*b*.—Lake Tulare	Tulare and Buena Vista lakes	Pacific Ocean, via San Joaquin R. (D); Monterey Bay drainage (A or C)??	Same as Pluvial, if existent	Sacramento system (conclusive); Monterey Bay drainage?
42*c*.—**Minor Coastal Stream Systems**	Various streams	Sacramento and Columbia rivers (A and C)	Uncertain	Sacramento and Columbia river faunas, modified
42*d*.—Lake Carrizo (not certainly Pluvial)	Carrizo Plain	None	Salinas R. (of Monterey Bay drainage)	Basin now fishless
Disrupted Parts of Columbia River System				
42*e*.—Fort Rock Lake	Silver Lake, Fossil Lake, desert about Fort Rock, etc.	Columbia R., via Long Prairie and Deschutes R. (D); Klamath R. system (C)?	Same as Pluvial?	Uncertain; probably Columbia R. and Klamath R. faunas; also other lake basins?
42*f*.—Lake Malheur	Malheur or Harney basin	Columbia R., via Malheur R. (D)	Part of Columbia R. system	Columbia system (conclusive)
42*g*.—Cow Lake (Postpluvial?)	Cow Lakes basin	Columbia R., via Owyhee R. (D)	Part of Columbia R. system	Columbia system (conclusive)
42*h*.—Crab Creek	Crab Creek basin	Columbia R. (D)	Part of Columbia R. system	Columbia system (conclusive)
42*i*.—Lake Moses	Moses Lake	Columbia R., via lower Crab Creek (D)	Part of Columbia R. system	Columbia system (presumptive)
42*j*.—Many other lakes	Other lakes on Channelled Scablands	Columbia R. (D)	Part of Columbia R. system	Basins unexplored by ichthyologists
Isolated streams of Snake River Lava Plateau				
42*k*.—Mud Lake-Lost River group	Five streams, in part tributary to Mud L. (p. 76)	None?	Part of Snake R. system	Columbia system (presumptive)
Wood R. group	Wood River and tributaries	Snake R.	Part of Snake R. system	Upper Snake system (conclusive)
42*l*.—Lava Lake (Postpluvial?)	Lava Lake	Wood R., via Fish Creek?	Uncertain	Basin now fishless
42*m*.—Fish Creek	Fish Creek	Part of Wood R. system	Same as Pluvial?	Upper Snake system (conclusive)
42*n*.—Wood River	Wood River	Snake R. (D)	Snake R. (D)	Upper Snake system (conclusive)
Death Valley System				
Mono Lake basin				
43.—Lake Mono	Mono Lake basin	Perhaps none, or with Owens R. (D)	First into Lahontan system, via Walker R. (D); then into Death Valley system, via Owens R. (D)	Basin now fishless

44.—Lake Aurora	Aurora Valley	Perhaps none	Probably first in outlet from L. Mono to Walker R.; later into L. Mono (D)	Basin now fishless
Owens River system				
45.—Long Valley Lake	Long Valley, in headwaters of Owens River	Owens R. (D)	Owens R. (D), if lake existent	Owens R. system (conclusive)
46.—Adobe Lake	Adobe Valley	Owens R., via North Fork (D)	Owens R., via North Fork (D)	Basin now fishless
47.—Lake Owens	Owens Lake basin	Death Valley, via lakes Searles and Panamint (D)	Death Valley, via lakes Searles and Panamint (D)	Lahontan and Colorado systems
Owens River-Death Valley connectives				
48.—Lake Searles, higher stage	Indian Wells-Searles basin	L. Panamint (D, in Tahoe time)	L. Panamint (D)	Basin now fishless
A.—Lake China	Indian Wells-Salt Wells Valley	L. Searles (D, in Tioga time)	Part of higher L. Searles	Basin now fishless
B.—Lake Searles, lower stage	Searles basin	None	Part of higher L. Searles	Basin now fishless
49.—Lake Panamint	Panamint Valley	Death Valley (D)	Death Valley (D)	Basin now fishless
50.—Lake Manly, Death Valley	Death Valley	None (D); Owens, Amargosa and Mohave systems (T)	Same as Pluvial; probably also Colorado R. (D)	Colorado system
Amargosa River system				
51.—Lake Tecopa	Middle part of Amargosa River drainage	Death Valley (D)	Death Valley (D); Las Vegas R., via Indian Springs L. (C)	Death Valley; Colorado system
52.—Lake Pahrump	Pahrump Valley	Amargosa R., via Ash Meadows (D)?	Amargosa R., via Ash Meadows (D)	Ash Meadows of Amargosa R. drainage (conclusive)
Mohave River system				
53. Lake Mohave	Playas of Soda and Silver dry lakes	Death Valley (D)	Death Valley (D); earlier, with Colorado R. (D)?	Mohave R.; remotely with Owens R.
54.—Little Lake Mohave	Cronise Valley	Pluvial Mohave R. (distributary)	Pluvial Mohave R. (distributary)?	Basin now fishless except when flooded by Mohave River
55.—Lake Manix	Middle part of Mohave River drainage	Lake Mohave, via Mohave R. (D)	Lake Mohave, via Mohave R. (D)	Mohave R.; remotely with Owens R.
56.—Small lakes in outlet of Lake Mohave	Outlet of Lake Mohave	Death Valley (D)	Death Valley (D)	Basins now fishless
Enclosed Fishless Basins Adjacent to Death Valley System				
57.—Lakes west of Mohave River				
A.—Lake Thompson	Antelope Valley	Lake Kane (D)	Lake Kane (D)?	Basin presumably fishless
B.—Lake Kane	Kane Dry Lake	Probably isolated	Possibly into Mohave R.	Basin now fishless
C.—Lake Harper	Harper Dry Lake	Probably isolated	Mohave R.	Basin now fishless
D.—Many other lakes, probably ephemeral	Dry lake basins west of Death Valley drainage	Probably none	Undetermined	Basins now all fishless
58. Lakes between Death Valley system and Fish Lake Valley				
A.—Deep Springs Lake, probably ephemeral	Deep Springs Valley	Presumably none	Possibly into Eureka Valley	Basin now fishless

Pluvial Lake or River	*Valley or Basin*	*Pluvial Connection (Abbreviations Explained on p. 147)*	*Most Plausible "Earlier Pluvial" Connection*	*Relationships of Recent Fish Fauna of Remnant Waters*
B.—Eureka Lake	Eureka Valley	Presumably none	Undetermined	Basin now fishless
C.—Saline Lake	Saline Valley	Presumably none	Undetermined	Basin now fishless
D.—Butte Lake	Butte Valley	Saline Valley?	Undetermined	Basin now fishless
59.—Lakes between Death Valley system and Colorado River				
A.—Lake Mesquite	Mesquite Dry Lake	Probably none	Pahrump Valley (D)?	Basin now fishless
B.—Lake Ivanpah	Ivanpah Dry Lake	Probably none	Probably none	Basin now fishless
C.—Lake probably ephemeral	Jean Dry Lake	Possibly Lake Ivanpah (D)	Lake Ivanpah?	Basin now fishless
D.—Lake probably ephemeral	Dry lake just east of Jean Dry Lake	Possibly Jean Dry Lake (D)	Lake Ivanpah?	Basin now fishless
E.—Lake probably ephemeral	Mesquite Dry Lake or Opal Mountain basin	Presumably none	Possibly Colorado R. (D)	Basin now fishless
a.—Lake Amboy (basin labeled F on map 1)	Bristol-Cadiz basin	Presumably none	Colorado R. (D)?	Basin now fishless
b.—Lake Ward	Danby basin	Presumably none	Colorado R. (D)?	Basin now fishless
c.—Several other lakes, probably ephemeral	Dry lake basins, SE. Mohave Desert	Undetermined	Undetermined	Basins now fishless
d.—Lake Lucerne	Lucerne Dry Lake	Probably none	Uncertain	Basin now fishless
60.—**Railroad Lake System**	Railroad Valley system (pp. 90-94)	None (D); possibly L. Lahontan (A or C)	Colorado R. (D)?	Lahontan and Colorado systems
Disrupted Parts of the Colorado River System				
White River and probably connected lakes				
61.—White River	White River Valley, etc.	Colorado R. (D)	Colorado R. (D)	Colorado system (conclusive)
62.—Coal Lake	Coal Valley	Possibly White R. (D)	White R.	Basin now fishless
63.—Lake Bristol	Bristol Valley	Probably White R., via L. Delamar (D)	White R., via L. Delamar (D)	Basin now fishless
64.—Lake Delamar	Delamar Valley	Probably White R. (D)	White R. (D)	Basin now fishless
Carpenter River and Lake Carpenter				
65.—Carpenter River	Meadow Valley Wash, etc.	Colorado R. (D)	Colorado R. (D)	Colorado system (conclusive)
66.—Lake Carpenter	Duck Valley	Carpenter R. (D)	Carpenter R. (D)	Basin now fishless
Las Vegas River and probably connected lakes				
67.—Las Vegas River	Las Vegas Valley	Colorado R. (D)	Colorado R. (D); Amargosa R., via Indian Springs L. (C)	Colorado system (presumptive)
68A-B.—Unnamed lakes, probably ephemeral	Mormon Gulch	Probably East L. (D)	East L. (D)	Basin now fishless
68C.—East Lake	East Dry Lake Valley	Las Vegas R. (D)	Las Vegas R. (D)	Basin now fishless
69.—Indian Springs Lake	Indian Springs Valley	Probably none	Las Vegas R. (D); Amargosa R. (C)	Basin now fishless
69*a.*—Lake Pinto and Pinto River	Pinto basin	Colorado R. (D) ?	Colorado R. (D)	Basin now fishless
Lakes LeConte, Clark and Pattie				
69*b.*—Lake LeConte (Lake Cahuilla)	Salton Sink	Colorado R. (distributary)	Colorado R. (distributary)	Colorado system (conclusive)
69*b′.*—Lake Clark	Clark Valley	None	L. LeConte	Basin now fishless
69*c.*—Lake Pattie	Pattie basin (Laguna Salada or Laguna Maquata)	Colorado R. (distributary)	Colorado R. (distributary)	Colorado system (conclusive)

Disrupted rivers and lakes on east side of Colorado River				
69*d*.—Sonoyta River	Sonoyta River	Colorado R. (D)	Colorado R. (D)	Colorado system (rather conclusive)
70.—Red Lake (existence in Pluvial time not certain)	Hualpai basin	Unknown	Unknown	Basin now fishless
70*a*.—Lake possibly Prepluvial	San Simon Valley	Colorado R., via Gila R. (D)	Colorado R., via Gila R. (D)	Colorado system
70*b*.—Lake Mormon	Mormon Lake	Unknown	Unknown	Fish fauna introduced
70*c*.—Red Desert lakes	Red Desert basin	Colorado R. (D) ?	Colorado R. (D) ?	Basin now fishless
70*d*.—Lake Animas	Animas Valley	Possibly Colorado R., via Gila R. (D)	Colorado R., via Gila R. (D)	Basin now fishless
Disrupted Parts of the Yaqui River System				
70*e*.—Lake Cochise	Cochise Valley	Yaqui R., via Whitewater R. (D); also possibly Colorado R., via Gila R. (C)	Yaqui R. and/or Colorado R. (D)	Insufficient fish data (see text, p. 115)
70*f*. Lake Cloverdale	San Luis Valley, N. M.	Presumably Yaqui R. (D)	Yaqui R. and/or Colorado R., via Gila R. (D)?	Basin now fishless
Disrupted Parts of the Rio Grande System in the United States				
70*g*.—Rio Mimbres	Rio Mimbres	Laguna de Guzman (D)	Laguna de Guzman (D)	Rio Grande (conclusive)
70*h*.—Lake Playas	Playas Lakes	L. Hachita (D)?	L. Hachita (D)?	Basin now fishless
70*i*. Lake Hachita	Hachita Valley	Laguna de Guzman (D)?	Laguna de Guzman (D)	Basin now fishless
70*j*.—Lake San Augustin	San Augustin Plains	Rio Grande (D)?	Rio Grande (D)	Basin now fishless
70*k*.—Lake Estancia and Encino	Estancia and Encino valleys	Rio Grande (D)?	Rio Grande (D)	Basin now fishless
70*l*.—Lake Otero	Tularosa Basin	Rio Grande (D)?	Rio Grande (D)	Rio Grande or Red R.
70*m*.—Salt Lakes	Salt Lakes Basin	Pecos R. (D)?	Pecos R. (D)	Basin now fishless
70*n*.—Coronado's Lakes	San Luis Valley, Colo.	Rio Grande (D)?	Rio Grande	Rio Grande (presumptive)

REFERENCES DEALING WITH THE PLUVIAL LAKES AND THE DISRUPTED STREAM SYSTEMS OF THE ARID PARTS OF NORTH AMERICA

This list supplements Table I. Outstanding contributions are indicated by bold-face type. An asterisk denotes the paper in which the given Pluvial water was formally named. The numbers and letters correspond with those given in the text, in Table I, and on map 1. Following the lake numbers capital letters are used to denote minor enclosed basins within the specified group and lower-case letters are inserted to denote lakes that are not within the area shown on map 1. The numbers given in parenthesis after the references to Meinzer (1922) and to Miller (1946*a*) are the lake numbers used on their maps. Entries are not made to authors whose treatment of a given lake consisted only in copying or slightly modifying the Pleistocene lake map of Meinzer or that of Russell (1885, 1889). Entries are not made to Young (1914), for the section that he took directly from Free (1914*a*).

Bonneville System (including Snake River above falls)

1.—Lake Bonneville (Great Salt Lake, Sevier Lake, Great American Desert and many other valleys in Utah and in adjacent parts of Nevada and Idaho).—Stansbury, 1852; Beckwith, 1855; **Gilbert,** 1875a,* **1882, 1890,** 1928; Howell, 1875; Simpson, 1876; Engelmann, 1876; King, 1878; Peale, 1879; Stearns, 1879; Whitney, 1882; Davis, 1883; Russell, 1885, 1889, 1902; Gardner and Stewart, 1900; Means, 1900; Gardner and Jensen, 1901*a–b;* Sanchez, 1904; Jensen and Strahorn, 1905; Richardson, 1906, 1907; Lee, 1908*b;* Meinzer, 1911*b,* 1922 (no. 41); Carpenter, 1913; Free, 1914*a*; Upham, 1914; Young, 1914; Lee, Stone, Gale and others, 1915; Nelson and Eckmann, 1916; Keyes, 1917*a–b,* 1918; Guernsey, Koeber, Zinn and Eckmann, 1919; Upham, 1922; Strahorn, Stucki and Jennings, 1925; Allee, 1926; Hay, 1927; Blackwelder, 1931; Fenneman, 1931, 1932; Boutwell, 1933; Hansen, 1933; Harrington, 1934*b*; Eardley, 1938; Stearns, Crandall and Steward, 1938; **Pack, 1939;** Jones, 1940; Hinds, 1943; Antevs, 1945; Miller, 1945*a*; Ives, 1946; Allison, 1946; Flint, 1947.

1*a*.—Bear Lake (in Utah and Idaho; tributary to Great Salt Lake).—Hayden, 1872; Peale, 1879; Mansfield, 1927; Jones, 1940; **Richardson, 1941.**

1*b*.—Little Salt Lake (Parowan Valley, Utah).—Gilbert, 1875; Meinzer, 1911*b*; Jones, 1940.

1*c*.—Pine Lake (Sage Brush Valley, Utah).—Jones, 1940.*

Lahontan System

2.—Lake Lahontan (Pyramid Lake, Walker Lake, Humboldt River, etc., Nevada; with arms in California and in Oregon).—Blake, 1872*a–b;* Engelmann, 1876; Hague, 1877*c** (name presumably taken from King, 1878); King, 1878; Whitney, 1882; **Russell, 1883,** 1884, **1885,** 1889, 1896; Louderback, 1904; Rutter, 1908; Strahorn and Van Duyne, 1912; Free, 1914*a*; Jones, 1914*a*; Snyder, 1914, 1917*a*; Young, 1914; Gale, 1915; Lee, Stone, Gale and others, 1915; Keyes, 1918; Waring, 1918; Guernsey, Koeber, Zinn and Eckmann, 1919; Meinzer, 1922 (no. 16); Antevs, 1925; Huntington, 1925; Jones, 1925, 1929; Hay, 1927; Loud and Harrington, 1929; Grinnell, Dixon and Linsdale, 1930; Blackwelder, 1931; Fenneman, 1931, 1932; Hutchinson, 1937; Sharp, 1938–1940; Jones, 1940; Hinds, 1943; Antevs, 1945; Miller, 1945*b*, 1946*a* (no. 2); Allison, 1946; Flint, 1947.

Pluvial Lakes Connected with Central Lahontan Basin

3.—Lake Newark and Fish Creek (Newark and Little Smoky valleys, in Nye, Eureka and White Pine counties, Nevada).—Russell, 1885, 1889; Spurr, 1903; Free, 1914*a*; Meinzer, 1922 (no. 42); present report.*

4.—Lake Diamond (Diamond, Kobeh, Monitor and Antelope valleys, in Eureka and adjacent counties, Nevada).—King, 1878; Hague, 1883; Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 36); Hubbs, 1941*a*.*

5.—Lake Gilbert (Grass Valley, in Lander County, Nevada).—Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 35); present report.*

6.—Lake probably "earlier pluvial" (Crescent Valley, in Lander and Eureka counties, Nevada).—King, 1878; Free, 1914*a*.

7.—Lake probably "earlier pluvial," with Pluvial remnant (Carico Valley, in Lander County, Nevada).—Hague, 1877*a*; King, 1878.

8.—Buffalo Lake (Buffalo Valley, in Lander County, Nevada).—King, 1878; Russell, 1885, 1889; Free, 1914*a*; Waring, 1918; Meinzer, 1922 (no. 20); present report.*

9.—Lake lacking or insignificant (Antelope Valley, Lander County, Nevada).—Waring, 1918.

10.—Lake Washoe (in recent time Big Washoe and Little Washoe lakes, Lyon County, Nevada).—**Russell,** 1883, **1885**, 1889; Reid, 1911; Snyder, 1917*a*; Meinzer, 1922 (no. 19); Hutchinson, 1937.

11A.—Lake Tahoe (on California–Nevada line).—LeConte, 1883–1884; Russell, 1883, 1885; Juday, 1907; Lee, Stone, Gale and others, 1915; Snyder, 1917*a*; Davis, 1933; Hinds, 1943.

11B.—Lake Truckee (in course of Truckee River, Sierra Nevada and Placer counties, California).—**Lindgren, 1898.**

12.—Eagle Lake (Lassen County, California).—Russell, 1885, 1889; Rutter, 1903; Free, 1914*a*; Snyder, 1917*a;* Meinzer, 1922 (no. 14); Grinnell, Dixon and Linsdale, 1930.

13.—Horse Lake (Lassen County, California).—Russell, 1885, 1889; Meinzer, 1922 (no. 15).

14.—High Rock Lake (on Humboldt–Washoe county line, Nevada).—Free, 1914*a*; **Russell, 1927a.***

15.—Lake Lemmon (Lemmon Valley, southern Washoe County, Nevada).—Free, 1914*a*; present report.*

Pluvial Lakes in Enclosed Basins Surrounded by Lahontan Watershed

16.—Lake Wellington (basin 11 to 13 miles north of Wellington, Lyon County, Nevada).—Present report.*

17A.—Lake Laughton (White Lake or Laughton Valley, southern Washoe County, Nevada).—Free, 1914*a*; present report.*

17B.—Lake Fred (basin east of Fred Mountain, southern Washoe County, Nevada).—Present report.*

18A.—Lake Kumiva (Kumiva or Kumavi Valley, northeast of Lake Winnemucca, Pershing County, Nevada).—King, 1878; Russell, 1883, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 17); Flint, 1947; present report.*

18B.—Granite Springs Lake (Granite Springs or Blue Wing Valley, east of Lake Winnemucca, Pershing County, Nevada).—King, 1878; Russell, 1883, 1885, 1889; Free, 1914*a;* Meinzer, 1922 (no. 18), present report.*

Minor Lakes Just South of Lake Lahontan System

19.—Fish Lake (Fish Lake Valley, Esmeralda County, Nevada).—Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 32); present report.*

20.—Lake Dixie (Humboldt Salt Marsh in Dixie or Osobb Valley, Churchill County, Nevada).—Hague, 1877*b*; King, 1878; Russell, 1885, 1889; Gale, 1913*a;* Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 21); Hubbs, 1941*a;* Flint, 1947; present report.*

21.—Lake Labou (Labou or Frenchman's Flat in Fair View Valley, Churchill County, Nevada).—Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 23); present report.*

22.—Lake Toiyabe (Big Smoky Valley, Nye and Lander counties, Nevada).—Russell, 1885, 1889; Free, 1914*a* ("Kingston Basin"); **Meinzer,** 1916,* **1917,** 1922 (no. 34); Hardman and Miller, 1934; Flint, 1947.

23.—Area of Sterile Basins

(All shown as no. 23 on map 1; general references: King, 1878; Russell, 1885; Bailey, 1902; Spurr, 1903; Chapman, 1906; Ransome, 1907; Ball, 1907; Schrader, 1913; Gale, 1913*a–b*; Free, 1914*a*; Carpenter, 1915; Meinzer, 1917, 1922; Hardman and Miller, 1934.)

A–G.—Basins Adjacent to Lake Lahontan

A.—Lake Edwards (Edwards Creek basin, Churchill County, Nevada).—King, 1878; Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 22); present report.*

B.—Lake Smith (Smith Valley, Lander County, Nevada).—King, 1878; Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 24); present report.*

C.—Lake Gabb (Gabbs Valley, Mineral County, Nevada).—Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 25); present report.*

D–D″.—Lakes Acme (D), Luning (D′) and Rhodes (D″) (Soda Springs Valley and Rhodes Salt Marsh, Mineral County, Nevada).—Russell, 1885, 1889; Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 30); present report.*

E.—Lake Garfield (Garfield Flat or Excelsior or Excellsior Flat, Mineral County, Nevada).—Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 29); present report.*

F.—Lake Teel (Teels Marsh, Mineral County, Nevada).—Free, 1914*a*; Young, 1914; present report.*

G.—Lake Huntoon (Huntoon Valley, Mineral County, Nevada).—Russell, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 28); present report.*

H–K.—Basins Structurally Connected with Basins of Lake Toiyabe and Fish Lake

H.—Lake Monte Cristo (Monte Cristo basin; lake near Mineral County border of Esmeralda County, Nevada; basin in both counties).—Free, 1914*a*.

I.—Lake Columbus (Columbus Salt Marsh, Esmeralda County, Nevada).—Russell, 1885, 1889; Free, 1914*a;* Young, 1914;; **Hicks, 1915***; Meinzer, 1922 (no. 31); Flint, 1947.

J.—Lake Tonopah (southern end of Big Smoky Valley, Esmeralda County, Nevada).—Dole, 1913; Free, 1914*a*; **Meinzer,** 1916,* **1917**, 1922 (no. 33); Flint, 1947.

K.—Lake Clayton (Silver Springs Marsh, Clayton Valley, Esmeralda County, Nevada).—Dole, 1913; Free, 1914*a*; Young, 1914; Meinzer, 1917; present report.*

L–T.—Basins Structurally Connected with Death Valley System (see general references above under Area of Sterile Basins). All with unnamed, probably ephemeral Pluvial lakes, in Nye and Esmeralda counties, Nevada

L.—Ralston Valley, leading to Mud Dry Lake.

M.—Salisbury Wash and Cactus Flat.

N.—Gold Flat.

O.—Alkali Spring Valley.

P–P′.—Northeastern and southwestern parts, respectively, of Stonewall Flat.

Q.—Basin west of Stonewall Flat (between Stonewall Flat and Clayton Valley).

R.—Sarcobatus Flat.

S.—Yucca Flat.

T.—Frenchman Flat.

U–V.—Basins Adjacent to Railroad Lake System (see general references, above, under 23). Lakes unnamed, probably ephemeral in Pluvial times; in Nye County, Nevada

U.—Willow Creek Basin.

V.—Kawich Valley.

W–Z.—Basins Structurally Connected with Pluvial White River (see general references above, under 23). Lakes unnamed, probably ephemeral in Pluvial times; in Nye, Lincoln and Clark counties, Nevada

W.—Penoyer or Sand Spring Valley.

X.—Papoose Dry Lake, Emigrant Valley.

X′.—Groom Dry Lake, Emigrant Valley.

Y.—Desert Valley.

Z.—Valley just north of Dry Lake Valley.

Z.′—Dry Lake Valley.

Lakes between Lahontan, Bonneville and Colorado Systems

24.—Lake Franklin (Ruby Valley and northern part of Butte Valley, Elko County, Nevada).—King, 1878; Russell, 1885, 1889; Gilbert, 1890; Free, 1914*a*; Clark and Riddell, 1920; Meinzer, 1922 (nos. 37 and 39); **Sharp, 1938***–1940; Flint, 1947.

25.—Lake Gale (southern part of Butte Valley, Elko and White Pine counties, Nevada).—Present report.*

26.—Clover Lake (Clover and Independence valleys, Elko County, Nevada).—King, 1878; Russell, 1885, 1889; Gilbert, 1890; Free, 1914*a*; Meinzer, 1922 (no. 38); Jones, 1940; present report.*

27.—Lake Steptoe (southern part of Steptoe Valley, Elko and White Pine counties, Nevada).—Russell, 1885 and 1889 (in part); Spencer, 1917; **Clark and Riddell, 1920***; Meinzer, 1922 (no. 43). Confused with L. Waring by Russell (1885).

28.—Lake Waring (northern part of Steptoe Valley, Elko County, Nevada).—Russell, 1885 and 1889 (in part); Free, 1914*a*; Lee, Stone, Gale and others, 1915; Clark and Riddell, 1920; Meinzer, 1922 (no. 40); Jones, 1940; present report.*

29.—Antelope Lake (Tippett basin of Antelope Valley, White Pine County, Nevada).—Clark and Riddell, 1920; Meinzer, 1922 (no. 44); Jones, 1940.*

30.—Spring Lake (Spring Valley, White Pine County, Nevada).—Cope and Yarrow, 1875; Free, 1914*a*; Clark and Riddell, 1920; Meinzer, 1922 (no. 45); Jones, 1940.*

31.—Lake probably small and ephemeral (Long or Murray Valley, White Pine County, Nevada).—Free, 1914*a*.

32.—Lake Jake (Jakes or White Sage Valley, White Pine County, Nevada). Miller and Alcorn, 1946; present report.*

Lakes North of Lahontan System

33.—Lake Madeline (Madeline Plains and Grasshopper Valley, Lassen County, California).—Russell, 1883, 1884, 1885, 1889; Rutter, 1903; Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 13); present report.*

34.—Lake Alvord (Virgin and Thousand Creek drainages in Humboldt County, Nevada, and Alvord Desert and connected valleys in Harney County, Oregon).—Blake, 1872*a–b;* Russell, 1884, 1885, 1889, 1903*a–b;* Davis, 1903; **Waring, 1909;** Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 7); Smith and Young, 1926*; Smith, 1927; Fuller and Waters, 1929; Fuller, 1931; Cressman, 1936, 1942; Hubbs and Miller, 1942; Flint, 1947.

34*a*.—Lake Mann (in northern arm of Alvord basin, Harney County, Oregon).—Same references (this lake and the next were shown on Meinzer's 1922 map as one dot, no. 8).

34*b*.—Juniper Lake (in northern arm of Alvord basin, Harney County, Oregon).—Same references.

35.—Summit Lake (Summit Lake basin, western Humboldt County, Nevada).—Free, 1914*a* (as part of Lahontan basin).

35*a*.—Lake Catlow (Catlow Valley, Harney County, Oregon).—Russell, 1884, 1885, 1889; Waring, 1909; Free, 1914*a*; Young, 1914; Meinzer, 1922 (no. 6); Smith and Young, 1926; Smith, 1927; Fuller and Waters, 1929; Fuller, 1931; **Cressman,** 1936, **1942*;** Hubbs and Miller, 1942; Flint, 1947.

36.—Guano Lake (Guano Lake basin, Lake County, Oregon, with tributaries in Washoe County, Nevada).—Russell, 1884, 1885, 1889; Free, 1914*a*; Meinzer, 1922 (no. 5); Fuller and Waters, 1929; Fuller, 1931; Cressman, 1936,* 1942.

37.—Lake Meinzer (Long Valley, northern Washoe County, Nevada).—**Russell, 1884**, 1885, 1889; Free, 1914*a*; Young, 1914; Meinzer, 1922 (no. 12); Cressman, 1942; present report.*

38.—Lake Surprise (Surprise Valley and Duck Flat, in Modoc and Lassen counties, California, and Washoe County, Nevada).—Cope, 1883; Russell, 1884, 1885, 1889; Free, 1914*a*; Young, 1914; Meinzer, 1922 (no. 11); **Russell, 1927b,*** 1928; Fuller, 1931; Jones, 1940; Flint, 1947.

39.—Lake Warner (Lake County, Oregon).—Cope, 1883; Russell, 1884, 1885, 1889; Snyder, 1908*b;* **Waring, 1908,** 1909; Van Winkle, 1914; Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 4); Fuller and Waters, 1929; Fuller, 1931; Cressman, 1942; Flint, 1947; Hansen, 1947; present report.*

40.—Cowhead Lake (not certainly a Pluvial lake; extreme northeastern Modoc County, California).—Present report.

40*a*.—Alkali Lake (Alkali Lake basin, northeastern Lake County, Oregon).—Snyder, 1908*b*; **Waring, 1908;** Van Winkle, 1914; Free, 1914*a*; Hubbs, 1941*a*.*

40*b*.—Lake Chewaucan (basins of Summer Lake, Chewaucan Marsh and Abert Lake, all in Lake County, Oregon).—Cope, 1883; Russell, 1884, 1885, 1889; Snyder, 1908*b*; **Waring, 1908;** Van Winkle, 1914; Free, 1914*a*; Young, 1914; Meinzer, 1922 (no. 2); Huntington, 1925*; Smith and Young, 1926; Fuller and Waters, 1929; Fuller, 1931; Cressman, 1942, 1946; Allison, 1945, 1946; Hansen, 1946, 1947; Flint, 1947.

41.—Klamath River System

41*a*.—Klamath Lakes (Upper and Lower Klamath lakes and Tule Lake, presumably connected; Clear Lake, possibly connected; shallow lakes over Klamath Marsh and over Sycan Marsh, Oregon and California, not connected).—Cope, 1879*b*; 1883; Russell, 1884, 1885, 1889; Seale, 1896; Gilbert, 1898; Evermann and Meek, 1898; Jordan, 1907; Snyder, 1908*c*; Sweet and McBeth, 1911; Van Winkle, 1914; Free, 1914*a;* Johnson, 1918; Meinzer, 1922 (no. 9); Gilbert, 1928; Fuller and Waters, 1929; Fuller, 1931; Peacock, 1931; Antevs, 1940; Cressman, 1942; Miller, 1945*b;* Hansen, 1947.

Caldera Lakes

41*b*.—Crater Lake (probably Postpluvial; Klamath County, Oregon).—Evermann and Meek, 1898; Van Winkle, 1914; Kemmerer, Bovard and Boormann, 1923; Atwood, 1935; Hasler, 1938; Hasler and Farner, 1942; **Williams, 1942**; Allison, 1945.

41*c*.—Medicine Lake (perhaps only Postpluvial; Siskiyou County, California).—Free, 1914*a;* Peacock, 1931; Anderson, 1941.

Disrupted Parts of Sacramento River System

42.—Goose Lake (Goose Lake basin, Modoc County, California, and Lake County, Oregon).—Cope, 1883; Russell, 1884, 1885, 1889; Snyder, 1908*b, c;* Rutter, 1908; Waring, 1908; Fowler, 1913; Van Winkle, 1914; Free, 1914*a*; Meinzer, 1922 (no. 10); Smith, 1927; Fuller and Waters, 1929; Fuller, 1931; Cressman, 1942.

42*a*.—Clear Lake (Clear Lake basin, Lake County, California).—Jordan and Gilbert, 1894; Smith, 1896; Holway, 1907; Coleman, 1930; **Davis, 1933**; Lindquist, Dionier and Hancey, 1943; Murphy, 1944.

42*b*.—Lake Tulare (Tulare and Buena Vista lake basins, California).—Blake, 1857; Evermann, 1906; Arnold and Anderson, 1910; Free, 1914*a*; Mendenhall, Dole and Stebler, 1916; Holmes, Eckmann, Nelson and Guernsey, 1921; Barbat and Galloway, 1934; Miller, 1946*a* (no. 1; in part); Flint, 1947.

42*c*.—Minor Coastal Stream Systems

(Various coastal drainages opposite the Sacramento and Columbia river systems in California, Oregon and Washington).—Snyder, 1905, 1908*a*, *c,* 1913, 1916; Branner, 1907; Holway, 1914; Davis, 1933.

42*d*.—Lake Carrizo (Soda Lake on Carrizo Plain, San Luis Obispo County, California).—Arnold and Johnson, 1909; Gale, 1913*d*; Free, 1914*a*; present report.*

Disrupted Parts of Columbia River System

42*e*.—Fort Rock Lake (Silver Lake, Paulina Marsh, Thorn Lake, Fossil Lake, Christmas Lake, lake beds about Fort Rock and adjacent drainage areas in Lake County, Oregon).—Cope, 1883, 1889; Russell, 1884, 1885, 1889; Shufeldt, 1892, 1913; Jordan, 1907; Snyder, 1908*b*; **Waring, 1908**; Van Winkle, 1914; Free, 1914*a*; Young, 1914; Meinzer, 1922 (no. 1); Huntington, 1925; Smith and Young, 1926; Smith, 1927; Hay, 1927; Fuller and Waters, 1929; Hodge, 1930; Fuller, 1931; Allison, 1940,* 1941, 1946; Dole, 1941; Cressman, 1942, 1946; Hansen, 1947.

42*f*.—Lake Malheur (Malheur or Harney basin, Harney County, Oregon).—**Russell, 1884**, 1885, 1889, 1903*a–b;* Snyder, 1908*b*; Waring, 1909; Van Winkle, 1914; Free, 1914*a*; Meinzer, 1922 (no. 3); Smith and Young, 1926; Smith, 1927; Fuller, 1931; Piper, Robinson and Park, 1939; anonymous, 1945; present report.*

42*g*.—Cow Lake (Cow Lakes basin, Malheur County, Oregon).—Russell, 1903*a*.

42*h*.—Crab Creek (Crab Creek system, eastern Washington).—Russell, 1893; Calkins, 1905; Evermann and Nichols, 1909; Schwennesen and Meinzer, 1918; Bretz, 1928, etc.; Flint, 1938.

42*i*.—Moses Lake (tributary to Columbia River via lower Crab Creek, Grant County, Washington).—Russell, 1893; Calkins, 1905; Schwennesen and Meinzer, 1918; Bretz, 1928, etc.; Flint, 1938.

42*j*.—Many other lakes (on Channelled Scablands of eastern Washington).—Russell, 1893; Free, 1914*a*; Bretz, 1928, etc.; Flint, 1938; Hansen, 1947.

42*k–n*.—Isolated Streams of the Snake River Lava Plain

42*k*.—Mud Lake–Lost River group (5 streams, in part tributary to Mud Lake, Jefferson, Clark and Butte counties, Idaho; see p. 76).—Russell, 1902; Stearns and Bryan, 1925; Stearns, Crandall and Steward, 1938.

Wood River group

42*l*.—Lava Lake (Butte County, Idaho).

42*m*.—Fish Creek (Butte County, Idaho).

42*n*.—Wood River (southern Idaho).—Gilbert and Evermann, 1894; Russell, 1902; Youngs, Trail and Young, 1933; Stearns, Crandall and Steward, 1938; Simon, 1942; Miller, 1945*a*.

Death Valley System

Mono Lake Basin

43.—Lake Mono (Mono Lake basin, Mono County, California, and Mineral County, Nevada).—Whitney, 1865; **Russell,** 1883, 1885,* **1889;** Free, 1914*a*; Young, 1914; Lee, Stone, Gale and others, 1915; Meinzer, 1922 (no. 26); Putnam, 1938, 1940; Vestal, 1942, 1943; Miller, 1946*a* (no. 3); Flint, 1947.

44.—Lake Aurora (Aurora Valley, Mineral County, Nevada).—**Russell,** 1885, **1889;** Free, 1914*a*; Meinzer, 1922 (no. 27); Miller, 1946*a*; present report.*

Owens River System

45.—Long Valley Lake (Long Valley, Mono County, California).—Spurr, 1903; Lee, 1906; Mayo, 1934*; Jenkins, 1938; Putnam, 1938, 1940; Miller, 1946*a* (no. 4); Flint, 1947.

46.—Adobe Lake (Adobe Valley, Mono County, California).—Free, 1914*a*; Gilbert, 1941; Miller, 1946*a** (no. 5); Flint, 1947.

47.—Lake Owens (Owens Valley proper, Inyo County, California).—Whitney, 1865; Gilbert, 1875*a*; Bailey, 1902; Lee, 1906; Trowbridge, 1911; **Gale,** 1913*a*, **1914***; Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 53); Louderback, 1923; Huntington, 1925; Blackwelder, 1933, 1934; Antevs, 1936; Schultz, 1937; Hinds, 1943; Miller, 1946*a* (no. 6); Flint, 1947.

Owens River–Death Valley Connectives

48.—Lake Searles, higher stage (Indian Wells-Searles basin, in Inyo, Kern and San Bernardino counties, California).—Russell, 1885 and 1889 (wrongly united with Lake Panamint); Bailey, 1902; **Gale,** 1913*a,** **1914***;* Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 54); Blackwelder, 1933, 1934, 1941; Jaeger, 1933, 1938; Miller, 1946*a* (no. 7); Flint, 1947.

A.—Lake China (Indian Wells Lake or China Lake, in Indian Wells–Salt Wells Valley, Inyo, Kern and San Bernardino counties, California).—Same references.

B.—Lake Searles, lower stage (Searles basin, Inyo and San Bernardino counties, California).—Same references.

49.—Lake Panamint (Panamint Valley, Inyo and San Bernardino counties, California).—Russell, 1885 and 1889 (wrongly united with Lake Searles); Bailey, 1902; **Gale,** 1913*a,** **1914;** Free, 1914*a;* Young, 1914; Meinzer, 1922 (no. 55); Blackwelder, 1933, 1934; Jaeger, 1933, 1938; Miller, 1946*a* (no. 8); Flint, 1947.

50.—Lake Manly (Death Valley, Inyo and San Bernardino counties, California).—Russell, 1885, 1889; Gilbert, 1890; Bailey, 1902; Free, 1914*a*; Young, 1914; Noble, 1926; Wales, 1930; Means, 1932*; **Blackwelder, 1933**, 1934; Jaeger, 1933, 1938; Hinds, 1943; Miller, 1943*a, b*, 1945*c*, 1946*a* (no. 9), in press; Flint, 1947.

Amargosa River System

51.—Lake Tecopa (southern Inyo County, California).—Bailey, 1902; Noble, 1926, 1931; Wales, 1930; Jaeger, 1933, 1938; Hardman and Miller, 1934; Blackwelder, 1934, 1936*; Miller, 1943*a*, 1946*a* (no. 10).

52.—Lake Pahrump (Pahrump Valley, in Inyo County, California, and southern tip of Nye County, Nevada).—Free, 1914*a*; Waring, 1920; Miller, 1943*b*, 1946*a** (no. 11).

Mohave River System

53.—Lake Mohave (sump of Mohave River, now Soda and Silver dry lakes, San Bernardino County, California).—Free, 1914*a*, 1916; Gale, 1914; Darton and others, 1915; Huntington, 1915; **Thompson**, 1921,* **1929**; Meinzer, 1922 (no. 59); Jaeger, 1933, 1938; Blackwelder, 1934; **Antevs, 1937; Bode, 1937; Campbell and Campbell, 1937**; Storie and Trussell, 1937; Hubbs and Miller, 1943; Miller, 1938*b*, 1946*a* (no. 14); Flint, 1947.

54.—Little Lake Mohave (Cronise Valley, just north of Mohave River, San Bernardino County, California).—Free, 1914*a;* **Thompson,** 1921,* **1929;** Meinzer, 1922 (no. 58); Jaeger, 1933, 1938; Hubbs and Miller, 1943; Miller, 1946*a* (no. 15); Flint, 1947.

55.—Lake Manix (in course of Mohave River, San Bernardino County, California).—**Buwalda, 1914***; Meinzer, 1922 (no. 57); Ellsworth, 1933; Jaeger, 1933, 1938; **Blackwelder and Ellsworth, 1936**; Miller and DeMay, 1942; Hubbs and Miller, 1943; Miller, 1946*a* (no. 16); Flint, 1947.

56.—Small lakes in outlet of Lake Mohave (same references as for Lake Mohave).

Enclosed Fishless Basins Adjacent to Death Valley System

57.—Lakes West of the Mohave River

A.—Lake Thompson (Rosamond, Buckhorn and Rogers, or Muroc, dry lakes in Antelope Valley, Kern and Los Angeles counties, California). —Russell, 1885, 1889; Johnson, 1911; Free, 1914*a*; Meinzer, 1922 (no. 56); Thompson, 1929; Miller, 1946*a** (no. 19).

B.—Lake Kane (Kane Dry Lake, Fremont basin, eastern Kern County, California).—Free, 1914*a*; Thompson, 1929; Miller, 1946*a** (no. 18).

C.—Lake Harper (Harper Dry Lake, western San Bernardino County, California).—Free, 1914*a*; Thompson, 1929; Jenkins, 1938; Miller, 1946*a** (no. 17).

D.—Many other lakes, probably ephemeral in Pluvial times (dry lake basins, other than that of Lake Harper, between the drainage basins of Lake Kane, including Lake Thompson, and of the Pluvial Owens and Mohave rivers, California).—Free, 1914*a*; Thompson, 1929; W. J. Miller, 1944.

58.—Lakes between Death Valley System and Fish Lake Valley

A.—Deep Springs Lake, probably ephemeral in Pluvial times (Deep Springs Valley, Inyo County, California).—Gilbert, 1875; Bailey, 1902; Free, 1914*a*; **Miller, 1928;** Myers, 1942; present report.*

B.—Eureka Lake, possibly only ephemeral in Pluvial times (Eureka Valley, Inyo County, California).—Bailey, 1902*; Free, 1914*a*; Chalfant, 1936.

C.—Saline Lake, possibly only ephemeral in Pluvial times (Saline Valley, Inyo County, California).—Bailey, 1902*; Free, 1914*a*; Young, 1914; R. R. Miller, 1944.

D.—Butte Lake, unconfirmed and perhaps of "earlier pluvial" age (Butte Valley, Inyo County, California).—Bailey, 1902*; Free, 1914*a* (as the "Racetrack"?, p. 41); Shuler, 1945.

59.—Lakes between Death Valley System and Colorado River

A.—Lake Mesquite, perhaps ephemeral (Mesquite Dry Lake, northeastern San Bernardino County, California).—Free, 1914*a*; Jenkins, 1938; Miller, 1946*a** (no. 12).

B.—Lake Ivanpah, perhaps ephemeral (Ivanpah Dry Lake, in San Bernardino County, California, and Clark County, Nevada).—Bailey, 1902*; Free, 1914*a*; Waring, 1920; Jenkins, 1938; Miller, 1946*a* (no. 13).

C.—Lake probably ephemeral (Jean Dry Lake, Clark County, Nevada).

D.—Lake probably ephemeral (dry lake just east of Jean Dry Lake, Clark County, Nevada).

E.—Lake probably ephemeral (Mesquite Dry Lake in Opal Mountain basin, Clark County, Nevada).—Free, 1914*a*.

a.—Lake Amboy (Bristol and Cadiz dry lakes, in Bristol Trough, San Bernardino County, California; northern tributaries shown, as F, on map 1).—Free, 1914*a*; **Thompson, 1929***; Blackwelder, 1933; Blackwelder and Ellsworth, 1936; Miller, 1946*a* (no. 20).

b.—Lake Ward (Danby Dry Lake, in Bristol Trough, San Bernardino County, California).—Free, 1914*a*; **Thompson, 1929*;** Blackwelder, 1933; Blackwelder and Ellsworth, 1936; Miller, 1946*a* (no. 21).

c.—Several other lakes, probably ephemeral in Pluvial times (dry lake basins in southeastern part of Mohave Desert, and in Colorado Desert, California; including Mesquite, Dale, and Palen lakes in the Mesquite Trough of Free, 1914*a*).—Brown, 1923; Thompson, 1929; Miller, 1946*a* (lakes shown but not numbered).

d.—Lake Lucerne, perhaps ephemeral (Lucerne Valley, San Bernardino County, California).—Hay, 1927; Miller, 1946*a* (unnumbered lake southwest of lake 16); present report.*

60.—Railroad Lake System

Railroad Lake and Tributaries (Railroad, Reveille, Warm Springs, Hot Creek and Fish Lake valleys, Nye County, Nevada).—Free, 1913, 1914*a*; Young, 1914; Carpenter, 1915; Lee, Stone, Gale and others, 1915; Meinzer, 1922 (no. 46); Hubbs, 1932, 1941*a**; Hardman and Miller, 1934; Flint, 1947.

Disrupted Parts of the Colorado River System

61–64.—Pluvial White River and Probably Connected Lakes

61.—White River (White River Valley, intervening valleys and canyons and Moapa River Valley, White Pine, Nye, Lincoln and Clark counties, Nevada).—Wheeler, 1875; Gilbert, 1893; Free, 1914*a*; **Carpenter, 1915**; Youngs and Carpenter, 1928; Longwell, 1928; Harrington, 1930; Hardman and Miller, 1934; Sumner and Sargent, 1940; Hubbs, 1941*a**; Hubbs and Miller, 1941; Sumner and Lanham, 1942; Tanner, 1942.

62.—Coal Lake, perhaps of independent drainage (Coal Valley, Lincoln County, Nevada).—Carpenter, 1915; Meinzer, 1922 (no. 48); present report.*

63.—Lake Bristol, perhaps of independent drainage (Bristol Valley, Lincoln County, Nevada).—Free, 1914*a;* Carpenter, 1915; Meinzer, 1922 (no. 49); present report.*

64.—Lake Delamar, perhaps of independent drainage (Delamar Valley, Lincoln County, Nevada).—Free, 1914*a*; Carpenter, 1915; Meinzer, 1922 (no. 50); present report.*

65–66.—Pluvial Carpenter River and Lake Carpenter

65.—Carpenter River (Meadow Valley Wash and tributary valleys, in Lincoln and Clark counties, Nevada, and Iron County, Utah).—Wheeler, 1875; Carpenter, 1915; Youngs and Carpenter, 1928; Hardman and Miller, 1934; Pack, 1939; present report.*

66.—Lake Carpenter (Duck Valley, northern Lincoln County, Nevada).—Carpenter, 1915; Meinzer, 1922 (no. 47); present report.*

67–69.—Pluvial Las Vegas River and Probably Connected Lakes

67. Las Vegas River (Las Vegas Valley, Clark County, Nevada).—Carpenter, 1915; Carpenter and Youngs, 1928; Hardman and Miller, 1934; Harrington, 1930, 1934*a;* Simpson, 1933; Rose, 1938; Miller, 1946*a*; present report.*

68A–B.—Unnamed lakes, probably ephemeral in Pluvial times (Mormon Gulch, Clark County, Nevada).—Free, 1914*a*.

68C.—East Lake (East Dry Lake Valley, Clark County, Nevada).—Free, 1914*a*; Carpenter, 1915; Meinzer, 1922 (no. 52); present report.*

69.—Indian Springs Lake (Indian Springs Valley, Clark County, Nevada).-Free, 1914*a*; Carpenter, 1915; Meinzer, 1922 (no. 51); Hardman and Miller, 1934; Miller, 1946*a*; present report.*

69*a*.—Lake Pinto and, later, Pinto River (eastern Riverside County, California).—Free, 1914*a*; Campbell and Amsden, 1934*; **Campbell and Campbell, 1935; Scharf, 1935**; Rogers, 1939; Hinds, 1943; Miller, 1946*a* (unnumbered streams and lakes south of lakes 20 and 21).

69*b–c*.—Lakes LeConte, Clark and Pattie

69*b*.—Lake LeConte (also known as Lake Cahuilla and as Blake Sea; Salton Sea basin, Colorado Desert, California and Baja California).—Blake, 1857, 1907, 1914; Stearns, 1879, 1901; Russell, 1885, 1889; Orcutt, 1890; Bailey, 1902*; Mendenhall, 1909*b*, 1910; Gale, 1913*a;* Free, 1914*a–b;* Jones, 1914; MacDougal, 1914; Ross, 1914; **Sykes,** 1914, 1926, **1937;** Lee, Stone, Gale and others, 1915; Evermann, 1916; Meinzer, 1922 (no. 60); **Brown**, 1922, **1923;** Strahorn, Watson, Kocher, Eckmann, and Hammon, 1922; Grinnell, 1926; Hanna, 1926; Buwalda and Stanton, 1930; **Kniffen, 1932**; Boutwell, 1933; Darton, 1933; Rogers, 1939; Leigh, 1941; Dill and Woodhull, 1942; Hinds, 1943; Miller, 1943*a,* 1946*a* (no. 22); Dill, 1944; W. J. Miller, 1944; Cockerell, 1945, 1946; Hilton, 1945; Flint, 1947.

69*b′*.—Lake Clark (Clark Valley, Imperial County, California).—Brown, 1923; present report.*

69*c*.—Lake Pattie (finally becoming Laguna Salada or Laguna Maquata; Pattie basin, northeastern Baja California).—Orcutt, 1890, 1891; Jordan and Richardson, 1907; MacDougal, 1907, 1917; Mendenhall, 1909; Free, 1914*a–b;* Grinnell, 1926; Sykes, 1926, 1937; **Kniffen, 1932;** Miller, 1943*a*.

69*d*–70*d*.—Disrupted Rivers and Lakes on East Side of Colorado River

69*d*.—Sonoyta River (along northwestern boundary of Sonora, Mexico).—Lumholz, 1912; Snyder, 1915; Bryan, 1925; Ives, 1936, 1942; Miller, 1943*a*.

70.—Red Lake (perhaps ephemeral; in Hualpai basin, Mohave County, Arizona).—Lee, 1908; Darton, 1910; Free, 1914*a*.

70*a*.—San Simon Valley (lake probably Prepluvial; in southeastern Arizona).-Schwennesen, 1917; Carpenter and Bransford, 1926.

70*b*.—Mormon Lake (perhaps ephemeral; near Flagstaff, Arizona).

70*c*.—Red Desert lakes (perhaps ephemeral; straddling the Continental Divide, Sweetwater County, Wyoming).—Smith, 1909; Ball, 1909; Schultz, 1909; Free, 1914*a*; Nace, 1939.

70*d*.—Lake Animas (Animas Valley, Grant County, New Mexico).—**Schwennesen, 1918***; Meinzer, 1922 (no. 62); Darton, 1933; Flint, 1947.

70*e–f*.—Disrupted Parts of the Yaqui River System

70*e*.—Lake Cochise (in Sulphur Spring basin, Cochise County, Arizona).—**Meinzer and Kelton, 1913***; Free, 1914*a*; Meinzer, 1922 (no. 61); Darton, 1933; Jones, 1940 (as Sulphur Spring Lake); Flint, 1947.

70*f*.—Lake Cloverdale (San Luis Valley, on New Mexico–Mexico border).—Huntington, 1914*; Free, 1914*a*; **Schwennesen, 1918;** Meinzer, 1922 (no. 64); Jones, 1940; Flint, 1947.

70*g–n*.—Disrupted Parts of the Rio Grande System

70*g*.—Rio Mimbres (between headwaters of Gila River and Rio Grande in New Mexico).—Free, 1914*a*; Darton, 1933.

70*h*.—Lake Playas (Playas Valley, Grant County, New Mexico).—Free, 1914*a*; Schwennesen, 1918*; Meinzer, 1922 (no. 63); Darton, 1933; Flint, 1947.

70*i*.—Lake Hachita (Hachita Valley and vicinity, along New Mexico–Mexico border).—Schwennesen, 1918; Meinzer, 1922 (no. 65); Darton, 1933; present report.*

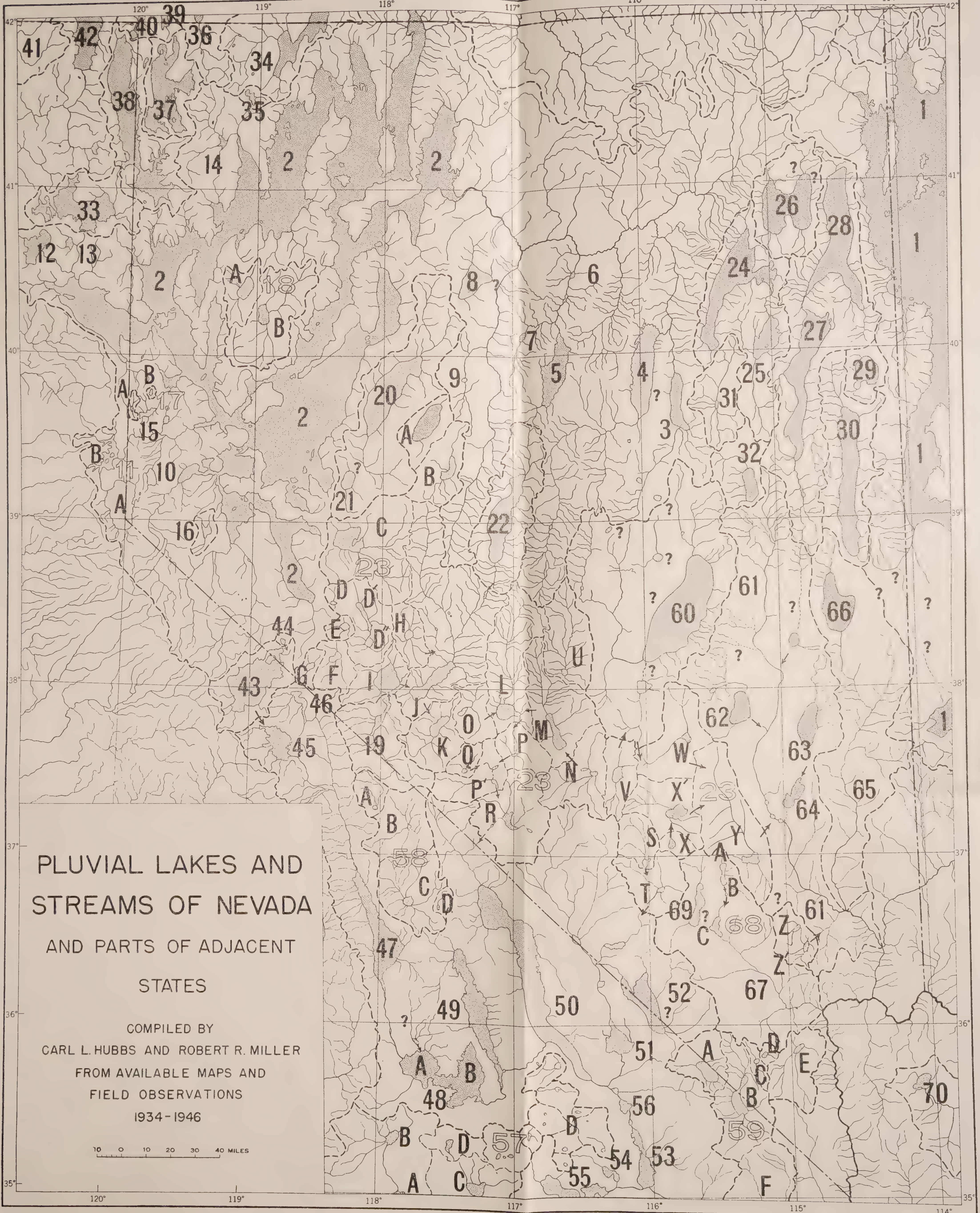
70*j*.—Lake San Augustin (San Augustin Plains, just east of the Continental Divide, Catron County, New Mexico).—Free, 1914*a*; Bryan, 1926*; Powers, 1933, 1939, 1941; Flint, 1947.

70*k*.—Lake Estancia and Lake Encino (in Estancia and Encino valleys, between the Rio Grande and Pecos River in central New Mexico).—Meinzer, 1911*a*, 1922 (nos. 66, 67); Free, 1914*a*; Antevs, 1935* (Estancia named); Flint, 1947; present report* (Encino named).

70*l*.—Lake Otero (Tularosa basin in south-central New Mexico.—Tarr, 1891; Herrick, 1904*; MacDougal, 1912; Free, 1914*a*; Huntington, 1914; Meinzer and Hare, 1915; Meinzer, 1922 (no. 68); Jones, 1940 (as Lake Tularosa); Blair, 1943; Flint, 1947.

70*m*.—Lakes in Sacramento River–Salt Lakes basin (southwestern New Mexico and northwestern Texas).—Fisher, 1906; Free, 1914*a*; Carter, Beck, Smith, Hawker, Templin and Reitch, 1928.

70*n*.—Coronado's Lakes in San Luis Valley (headwater area of Rio Grande in Colorado).—Stevenson, 1875; Endlich, 1877; Whitney, 1882; Jordan, 1891*a*; Holmes, 1904; Siebenthal, 1910; Free, 1914*a*; Ramaley, 1942.



PLUVIAL LAKES AND STREAMS OF NEVADA AND PARTS OF ADJACENT STATES

COMPILED BY CARL L. HUBBS AND ROBERT R. MILLER FROM AVAILABLE MAPS AND FIELD OBSERVATIONS 1934-1946

42°
41°
40°
39°
38°
37°
36°
35°
120°
119°
118°
117°
116°
115°
114°
10 0 10 20 30 40 MILES
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40
39
36
34
38
37
35
14
2
33
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A
B
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Contribution No. 370

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Printed in U. S. A.

California Stratus Forecasting Correlations, 1935 and Other Years*

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ONE OF THE MORE INTERESTING articles on California stratus† is that published in the February 1938 issue of the *Bulletin of the American Meteorological Society* by Petterssen, entitled "On the Causes and the Forecasting of the California Fog." In that discussion it was concluded that stratus at San Diego is of a convective nature and that therefore certain relationships may be expected. For example, the base of the stratus layer should coincide with the condensation level of the surface particles. Also, stratus could only be present when the condensation level of the surface air particles is lower than the base of the inversion. Thus, if the base of the inversion be assumed to be the cloud top, then the difference in height between the inversion base and the condensation level (BI–LCL) should correspond to the cloud thickness. Petterssen's data show: (*1*) that all cases of unbroken stratus occurred when the condensation level was below the base of the inversion, (*2*) that scattered stratus occurred when the condensation level was close to the base of the inversion, and (*3*) that all cases without stratus occurred when the condensation level was higher than the base of the inversion.

Petterssen suggested that, if stratus is of a convective nature, it should burn off early when the distance BI–LCL is small (thin stratus layer) and late when this distance is large (thick stratus layer). He mentioned that the time stratus breaks depends on other factors as well as upon cloud thickness. For example, when the inversion base is high the diurnal amplitude of temperature at any level below the base will be small and the effect of this small temperature variation upon dissolving of stratus will not be as great as the effect of the larger temperature variation which occurs with a lower inversion.

If the thickness of the stratus depends upon the height of the inversion base and upon the height of the condensation level, the normal variation of these two quantities is important. Petterssen computed their average diurnal variation and stated that the diurnal variation in the height of the inversion base was negligible. However, he presented data which indicated that the direction of the air current under the inversion brought about significant non-diurnal changes in the height.

Since Petterssen's study was made, the radiosonde has been placed in service and much additional data now are available. Some of these data have been collected at Scripps Institution for use in a fog-forecasting project under the Office of Naval Research. The data for San Diego have been compiled in a form similar to that used by Petterssen in order that a comparison may be made between his results using 1935 data and results using similar data from 1943, 1944, and 1945.

If the correlations noted in 1935 could be assumed to hold for all years, the forecasting of California stratus would be much simplified. However, it appears that Petterssen's study was based upon a relatively short period (57 days) when weather conditions were unusually stagnant and that the correlations worked out for this period cannot be assumed to hold as well in other periods. The same general tendencies appear, but they are not always as marked.

For first comparison, other periods of approximately the same length and weather conditions as the period in 1935 were selected. These periods were July 10 through September 12, 1944, and June 9 through

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* (Prepared at Scripps Institution of Oceanography, University of California, August 8, 1947. The work represents results of research carried out for the Office of Naval Research, Navy Department, under contract with the University.) Contribution from the Scripps Institution of Oceanography, New Series, No. 370.

† In accordance with common usage the term 'California Fog' was used by Petterssen although he stated that the term 'California Stratus' would be more adequate. The latter is used here except in direct quotations from Petterssen.

August 3, 1945. To increase the number of observations for the statistical study, the three six-month periods from May through October in 1943, 1944, and 1945 were also used.

Cloud thickness was calculated in accordance with Petterssen's method by subtracting the height of the lifting condensation level (LCL) from the height of the inversion base (BI). Following are correlation coefficients relating calculated thickness of overcast at the time of the morning raob with hour of breaking of the overcast:

1935*	0.84	1943 (6 months)	0.36
1944 (65 days)	0.47	1944 (6 months)	0.17
1945 (56 days)	0.13	1945 (6 months)	0.05

* All 1935 data are reproduced from Petterssen's discussion. Computations for 1943, 1944, and 1945 were carried out by Miss Margaret Culbertson.

TABLE I shows the relation between calculated cloud thickness and observed sky cover below the inversion at time of the morning sounding.

TABLE II gives the average diurnal surface-temperature range at Lindbergh Field corresponding to given morning inversion heights.

A comparison between average lifting condensation levels at 0600 and 1500 PST, which are near the time of minimum and maximum respectively, is given in TABLE III.

A tabulation was made to show the average height of inversion base with different surface wind directions, see TABLE IV.

Finally, the average variation in height of inversion base between morning and evening observations was computed and found to be 104 meters duiurg the 65-day

TABLE I.—FREQUENCIES OF SKY COVERS BELOW THE INVERSION AT DIFFERENT VALUES OF CALCULATED CLOUD THICKNESS (BI-LCL)

(BI-LCL) (100s of meters)	Sky Cover at Raob Time														
	1935			1944 (65 days)				1945 (56 days)				1943–45 (18 months)			
	O[1]	S[3]	C[4]	O	B[2]	S	C	O	B	S	C	O	B	S	C
>12 —												11		4	1
11 to 12												5	1	1	
10 to 11															2
9 to 10												5		1	
8 to 9												3		1	
7 to 8								1				9	3		
6 to 7								1				12	2	2	
5 to 6				3				1	1			19	2	1	
4 to 5				3				1				24	3	1	4
3 to 4	3			9				10				57	7	3	3
2 to 3	9	1		16		1		6		1		65	4	3	2
1 to 2	7			17	1	1	1	9			2	92	4	4	7
0 to 1	8	5		4	1		1	9		1	1	49	3	3	10
−1 to 0			1		1		3	3				16	5	1	10
−2 to −1			5					2		1	1	4	4	2	9
−3 to −2			4					1			2	2	1	2	7
−4 to −3			2				1						1		9
<−4			12										1		23

[1] O = overcast; [2] B = broken (.6–.9 sky covered); [3] S = scattered (.1–.5); [4] C = clear.

period in 1944, 106 meters during the 56-day period in 1945, and 90 meters for the eighteen-month period consisting of the six summer months from May through October in each of the three years 1943, 1944, and 1945. Thus the diurnal variation was at least twice that (40 meters) quoted by Petterssen.

Table II.—Average Diurnal Surface Temperature Range with Different Heights of Inversion Base

Morning Height of Inversion Base (meters)	Diurnal Surface-Air-Temperature Range (°F)			
	1935	1944 (65 days)	1945 (56 days)	1943–45 (18 months)
0– 50	23	20 (1)†	— (0)	22 (31)
0– 100	17	20 (4)	— (0)	22 (38)
100– 200	14	20 (2)	13 (5)	18 (41)
200– 300	10	15 (5)	11 (4)	15 (41)
300– 400	9	16 (13)	13 (9)	15 (67)
400– 500	7	13 (7)	12 (8)	14 (62)
500– 600	7	12 (11)	11 (13)	12 (67)
600– 700	7	13 (8)	10 (4)	12 (48)
700– 800	8	12 (5)	8 (2)	12 (27)
800– 900	1	12 (5)	10 (4)	12 (35)
900–1000		12 (2)	10 (1)	11 (19)
1000–1100		11 (1)	— (0)	11 (23)
1100–1200			11 (1)	11 (15)
1200–1300			10 (2)	11 (11)
1300–1400			14 (1)	11 (3)
1400–1500				11 (5)
1500–2000				12 (22)
2000–3000				13 (6)

† Figures in parentheses indicate number of cases.

Table III.—Average Lifting Condensation Level at 0600 and 1500 PST

Time	Average Lifting Condensation Level (meters)			
	1935	1944 (65 days)	1945 (56 days)	1943–45 (18 months)
0600	500	316	353	378
1500	963	905	866	924

Sea-surface isotherms for particular times based on data collected by the *E. W. SCRIPPS* show patterns in the San Diego area which are quite different from the patterns of average isotherms of Thorade which Petterssen used. For an example, see the chart for August 16–26, 1938, Figure 1. Observations were made where dots appear. Many cruises have shown that the pattern of isotherms in Figure 1 is not unusual but that its main features are typical of the area covered. Upon the 1938 isotherms in Figure 1 are superimposed in dashed lines the isotherms of Thorade which were included in Petterssen's study.

It is apparent that a pattern of sea-surface isotherms such as that which existed in August, 1938 would have considerable influence on formation and dissipation of stratus and upon the ceiling height. With westerly or northwesterly airflow, since cloudiness increases and ceiling lowers when there is surface cooling, it would be expected that the regions where the sea-surface temperature is below 63°F would have more extensive cloud cover and lower ceilings than the region just west of San Diego where the sea temperatures are as high as 70°. If a sufficiently thick layer of stratus were formed over the region of coldest water, the layer might be carried to San Diego before being entirely dissipated by the heating from below. The ceiling would gradually rise as the air moved toward San Diego and the cloud cover would extend inland for a distance which would depend on the temperature of the land surface, the tempera-

Table IV.—Average Height of Inversion Base with Different Wind Directions

Wind Direction	Average Height of Inversion Base (meters)			
	1935	1944 (65 days)	1945 (56 days)	1943–45 (18 months)
N	210	437 (41)	503 (20)	518 (280)
E	200	600 (8)	538 (18)	692 (111)
S	640	657 (17)	559 (14)	708 (122)
W	450	490 (27)	478 (18)	641 (193)

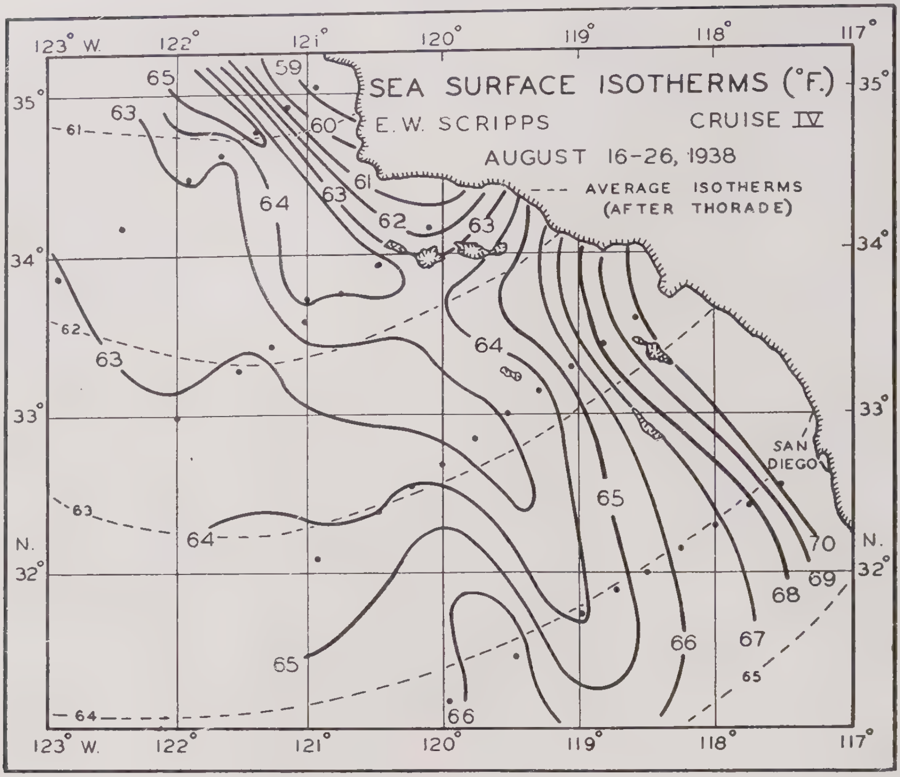
SEA SURFACE ISOTHERMS (°F.)
E. W. SCRIPPS
CRUISE IV
AUGUST 16-26, 1938
--- AVERAGE ISOTHERMS (AFTER THORADE)
SAN DIEGO
123° W.
122°
121°
120°
119°
118°
117°
35°
34°
33°
N.
32°
59
60
61
62
63
64
65
66
67
68
69
70

FIGURE 1

ture of air above it, and the strength of the onshore airflow.

The new sea-surface temperature data indicate that the role of this factor in stratus formation should be re-evaluated. It has been evaluated for surface fog at San Diego and the results summarized in a recent Scripps Institution Oceanographic Report titled "Sea Surface Temperature Variations Influencing Fog Formation in Southern California."

The compilations and comments above serve to strengthen some of the arguments presented by Petterssen and to weaken others. They indicate that the problem of stratus forecasting is not a simple one but is one which requires further intensive investigation. Indications are that some of the results of the fog-forecasting project at Scripps Institution will be applicable to stratus.

Contribution No. 371

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DIFFRACTION OF WATER WAVES BY BREAKWATERS

J. A. Putnam and R. S. Arthur

(Contribution from the University of California, Fluid Mechanics Laboratory Publication No. HE-116-280, and the Scripps Institution of Oceanography, New Series, No. 371)

Abstract--Application is made of a solution of the water-wave diffraction problem of Penny and Price to diffraction by a semi-infinite impermeable breakwater. Approximations are introduced to simplify application of the theory. Comparison of complete and simplified solutions is made with results obtained from a laboratory investigation. Best agreement between theory and experiment occurred in the lee of the breakwater. The simplified solution is shown to be adequate for most practical applications.

Introduction

Wave diffraction is considered here to be the phenomenon in which water waves are propagated into a sheltered region formed by a breakwater or similar barrier which interrupts a portion of an otherwise regular wave train. A knowledge of diffraction behavior has important application in the design and location of breakwaters in connection with harbor development. It would also appear to have a bearing on the distribution of wave energy along beaches located in the lee of headlands and offshore islands.

The sheltering effect of a breakwater of finite length and vertical impermeable walls depends upon diffraction of the incident waves around the ends of the breakwater. The phenomenon is quite analogous to the diffraction of light and a theory of breakwater diffraction has been adapted from the theory of physical optics. This paper presents a review of the theory and comparison is made with the results of experiments which were carried out with a view toward confirmation of this theory.

Theory

PENNY and PRICE [1944] have shown that Sommerfeld's solution of the optical diffraction problem [BATEMAN, 1944, pp. 476-485] is also a solution of the water-wave diffraction problem. The following discussion deals with a form of the solution which is modified from the original, and which appears to be particularly adapted to the present application.

Solution for progressive waves without a barrier present--A treatment of progressive waves is given in considerable detail by LAMB [1932, pp. 363-369]. Assume a cylindrical co-ordinate system with r and θ in the plane of the undisturbed water surface as shown in Figure 1, and the z-axis vertically upwards. Let η be the elevation at time t of the water surface above the undisturbed level.

The following assumptions are made regarding the wave motion and the boundary conditions: (1) The motion is irrotational and the velocity potential therefore satisfies Laplace's equation; (2) the motion is infinitely small; (3) at a fixed boundary the normal component of the fluid velocity is zero; (4) at the free surface the pressure is constant; and (5) the water is of uniform depth h.

Under these assumptions the expression for the surface elevation is of the form

$$\eta = (AikC/g)e^{ikCt} \cosh kh \cdot \mathbf{F}(r, \theta) \quad \ldots \ldots (1)$$

where $i = \sqrt{-1}$ but only the real part is to be finally retained and where $\mathbf{F}(r, \theta)$ satisfies the equation

$$(\partial^2 F/\partial r^2) + (1/r)(\partial F/\partial r) + (1/r^2)(\partial^2 F/\partial \theta^2) + k^2 F = 0 \quad \ldots \ldots (2)$$

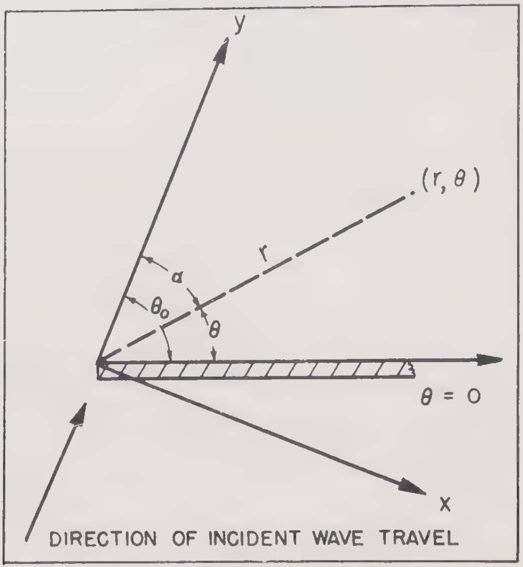


Fig. 1--Nomenclature for wave diffraction analysis

The meaning of the constants A, k, and C is best illustrated by considering the case of progressive waves traveling in the direction $\theta = \theta_0$ for which

$$F(r, \theta) = e^{-ikr \cos(\theta_0 - \theta)} \quad \ldots\ldots (3)$$

and the resulting waves have the following properties:

Length = $L = 2\pi/k$
Period = $T = 2\pi/kC$
Amplitude = $a = (AkC/g) \cosh kh$
Velocity = $C = \sqrt{(g/k) \tanh kh}$

Solution with a barrier present--The additional boundary condition imposed by the barrier must also be satisfied. Assume a barrier in the form of a rigid breakwater extending from the origin along the initial line $\theta = 0$.

To determine the nature of the diffracted waves it is necessary to obtain a solution of (2) for which the normal component of the fluid velocity is zero along the breakwater and which reduces to (3) for large values of r when $\theta = 180°$. Sommerfeld obtained such a solution for the diffraction of light by a semi-infinite screen in the case where the light is polarized in a plane parallel to the edge of the screen [BATEMAN, 1944, p. 484].

$$F(r, \theta) = (1/\sqrt{2})\, e^{i[(\pi/4) - kr\cos(\theta_0 - \theta)]} \int_{-\infty}^{u_1} e^{-i\pi v^2/2}\, dv$$

$$+ (1/\sqrt{2})\, e^{i[(\pi/4) - kr\cos(\theta_0 + \theta)]} \int_{-\infty}^{u_2} e^{-i\pi v^2/2}\, dv \quad \ldots\ldots (4)$$

where

$$u_1 = -\sqrt{4kr/\pi}\, \sin[(\theta_0 - \theta)/2] \text{ and } u_2 = -\sqrt{4kr/\pi}\, \sin[(\theta_0 + \theta)/2] \quad \ldots\ldots (5)$$

The dependence of the surface elevation η upon solution (4) can now be investigated. Since $F(r, \theta)$ is a complex number it can be written in the form

$$F(r, \theta) = \rho(r, \theta)\, e^{i\phi(r, \theta)} \quad \ldots\ldots (6)$$

where $\rho(r, \theta)$, the modulus of $F(r, \theta)$ is hereafter denoted by the symbol $|F(r, \theta)|$, and $\phi(r, \theta)$, the argument of $F(r, \theta)$, is hereafter denoted by arg $F(r, \theta)$. Substitution of (6) in (1) leads to the expression

$$\eta = (AkC/g) \cosh kh \cdot |F(r, \theta)|\, e^{i[(\pi/2) + kCt + \arg F(r, \theta)]} \quad \ldots\ldots (7)$$

where only the real part is to be retained. Equation (7) shows that the modulus of $F(r, \theta)$ determines the amplitude of the diffracted waves, and that the argument determines the wave pattern. A diffraction factor, K′, is now defined to be the diffracted wave height divided by the incident wave height, in analogy to the refraction factor, K [MUNK and TRAYLOR, 1947]. From (1), (3), and (7)

$$K' = (2AkC/g) \cosh kh \cdot |F(r, \theta)| / [(2AkC/g) \cosh kh] = |F(r, \theta)| \quad \ldots\ldots (8)$$

Complete solution for $F(r, \theta)$--For the complete evaluation of $F(r, \theta)$ a function f(u) is defined as

$$f(u) = (1/\sqrt{2})\, e^{i\pi/4} \int_{-\infty}^{u} e^{-i\pi v^2/2}\, dv \quad \ldots\ldots (9)$$

The modulus and argument of f(u) can be determined from tabulated values of the Fresnel integrals, C(u) and S(u) [JAHNKE and EMDE, 1943, pp. 34-36]; for $u > 0$

$$C(u) - iS(u) = \int_0^u e^{-i\pi v^2/2}\, dv \quad \ldots\ldots (10)$$

For $u < 0$, the relationship $f(-u) = 1 - f(u)$ which can be derived from (9) is useful. The modulus and argument of f(u) are represented graphically in Figure 2, and since the integrals in solution (4) can be expressed in terms of $f(u_1)$ and $f(u_2)$, a complete evaluation of $F(r, \theta)$ is possible. The labor involved in computations can be reduced by the introduction of approximations.

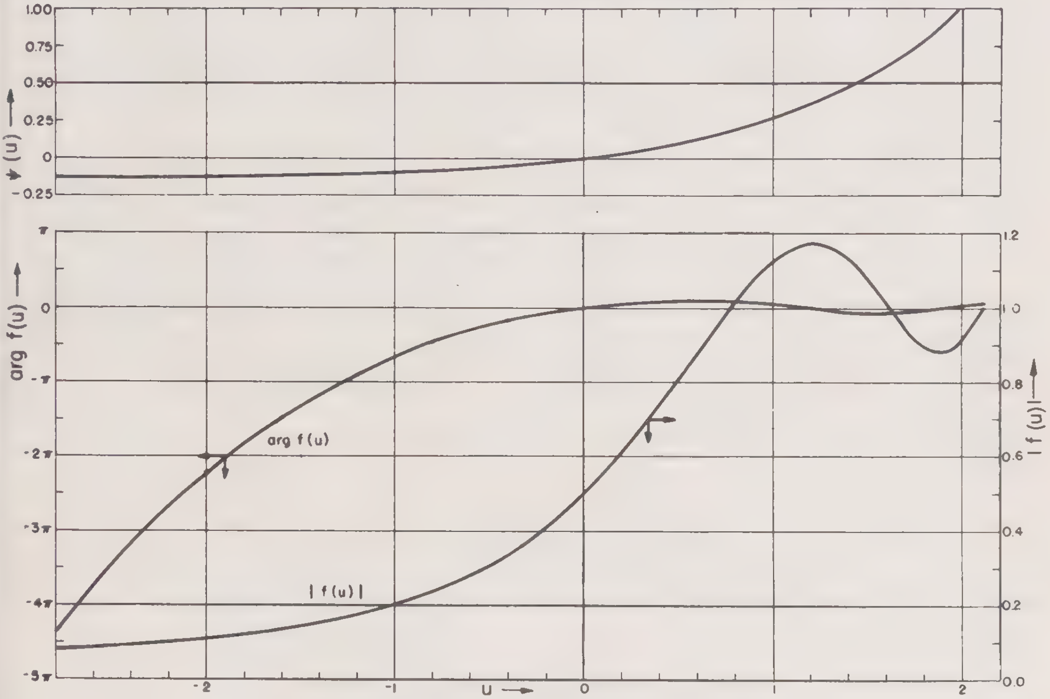


Fig. 2--Functions of u: Ψ(u), arg f(u), and mod f(u)

For $u < -2$ it is possible to use the approximation [BATEMAN, 1944, p. 483]

$$f(u) \cong -(1/\pi\sqrt{2}\, u)\, e^{-i\pi[(1/4) + (u^2/2)]} \quad \ldots\ldots (11)$$

The value of u_2 which occurs in (4) is less than -2 for the greater part of the region beyond the breakwater. After introduction of $f(u_1)$ and $f(u_2)$ for the integrals and approximation of $f(u_2)$ by (11), expression (4) can be written in the form

$$F(r, \theta) = \left\{ |f(u_1)| - (1/\pi\sqrt{2}\, u_2)\, e^{-2\pi i[(1/8) + \Psi(u_1)]} \right\} e^{-2\pi i[(r/L) - \Psi(u_1)]} \quad \ldots (12)$$

where (assuming $u_2 < -2$)

$$u_1 = -\sqrt{8r/L}\, \sin[(\theta_0 - \theta)/2]$$

$$u_2 = -\sqrt{8r/L}\, \sin[(\theta_0 + \theta)/2]$$

$$\Psi(u) = (u^2/4) + \left\{ [\arg f(u)]/2\pi \right\}$$

Ψ(u) is represented graphically in Figure 2.

Evaluation of K′ can be accomplished from (12), since it will be recalled that K′ equals the modulus of $F(r, \theta)$ which in this case is the modulus of the first factor on the right-hand side of (12). This modulus is obtained graphically by representing each of the two terms in the first factor as vectors and combining vectorially. The argument when added to the argument of the second factor gives the argument of $F(r, \theta)$.

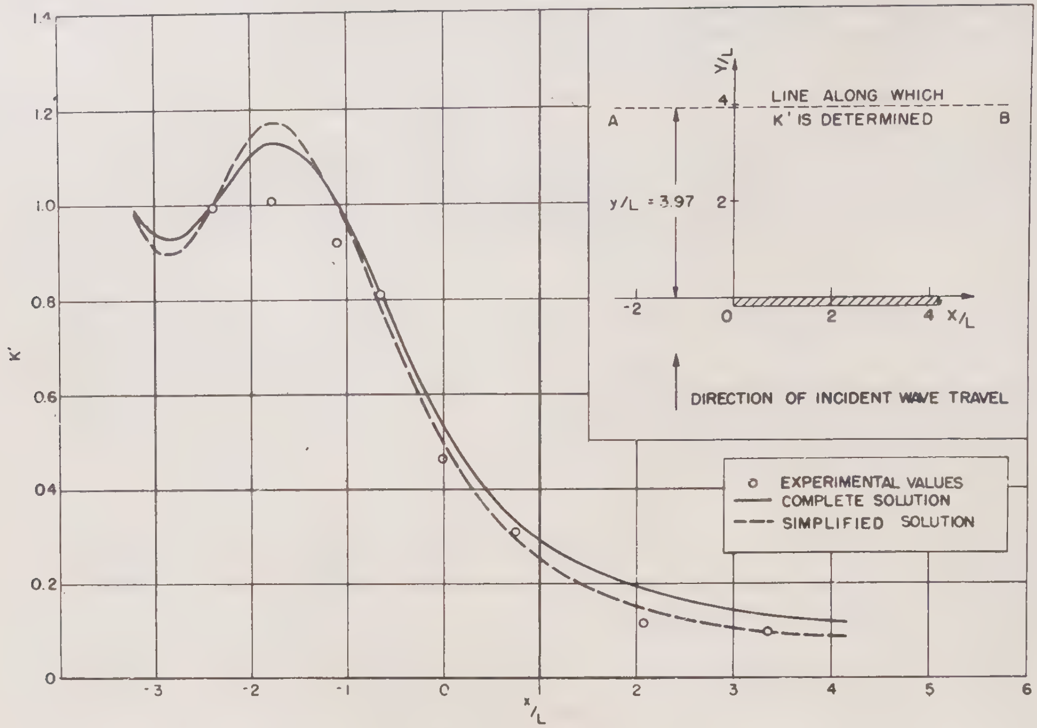


Fig. 3--Comparison of the simplified solution with the complete solution of the water-wave diffraction problem

In certain parts of the region beyond the breakwater, (12) can be further simplified to forms utilized in optical diffraction. The results for three such special cases follow:

Case 1: $u_1 = 0$, $(\theta = \theta_0)$

$$F(r, \theta) = [(1/2) - (1/\pi\sqrt{2}\, u_2)\, e^{-\pi i/4}]\, e^{-2\pi i r/L} \quad \ldots\ldots (13)$$

Case 2: $u_1 < -2$

$$F(r, \theta) = [-(1/\pi\sqrt{2}\, u_1) - (1/\pi\sqrt{2}\, u_2)]\, e^{-2\pi i[(r/L) + (1/8)]} \quad \ldots\ldots (14)$$

Case 3: $u_1 > 2$

$$F(r, \theta) = \left\{1 + (1/\pi\sqrt{2})\, [(1/u_1) + (1/u_2)]\, e^{-2\pi i\, [(u_1^2/4) - (3/8)]}\right\} e^{-2\pi i\, [(r/L) - (u_1^2/4)]} \quad \ldots (15)$$

The curve labeled "complete solution" in Figure 3 has been computed by use of these approximations when appropriate.

Simplified solution--The second term in the first factor of (12) can be completely neglected when its modulus is small compared to $|f(u_1)|$. However, this will not be the case if (r/L) is small, or if 2 is small as shown in Figure 3. If this simplification of ommitting the second term in (12) is introduced it is convenient to transform back to rectangular co-ordinates by means of the relationships $y = r \cos (\theta_0 - \theta)$ and $x^2 + y^2 = r^2$. The resulting expression can be written in the form

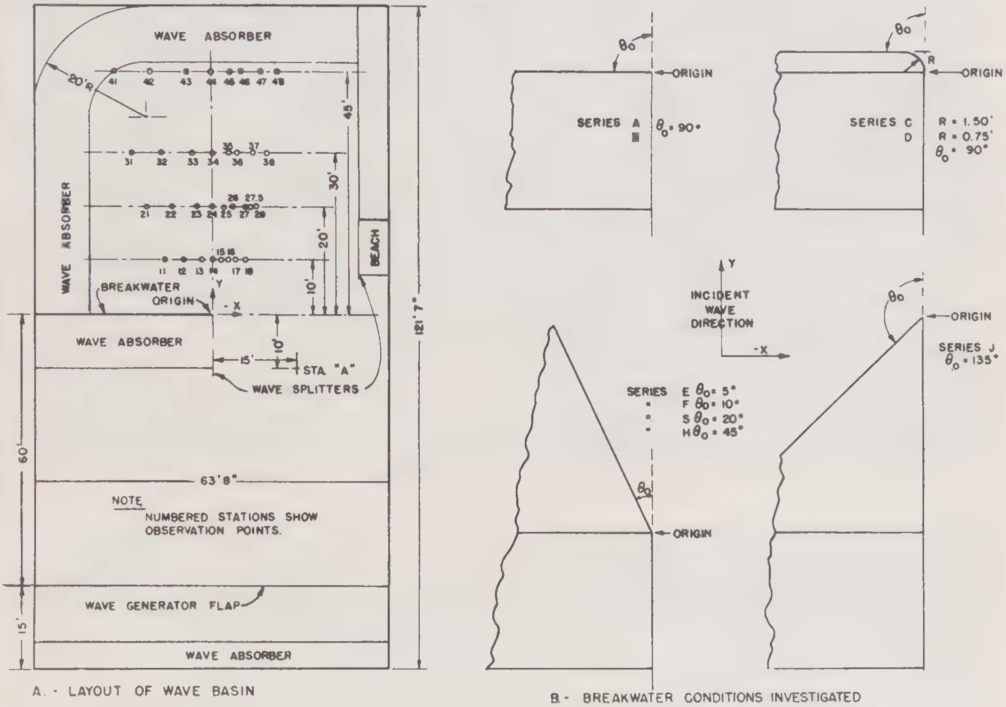
$$F(x, y) = e^{-2\pi i y/L} \cdot f(u_1) \quad \ldots\ldots (16)$$

where

$$u_1^2 = (4/L)\,(\sqrt{x^2 + y^2} - y) \quad \ldots\ldots (17)$$

and the sign of u_1 is to be determined by reference to the expression for u_1 given in (5). The curve labeled "simplified solution" in Figure 3 has been computed by this method.

Barrier of finite length--No exact solution has been found for the case of a barrier of finite length. It is believed that satisfactory results can be obtained by using a solution of the type indicated above for each end of the barrier. The co-ordinate systems assigned to each end must be mirror images of each other. The waves diffracted from the two edges will produce an interference pattern beyond the barrier, and the maximum height of the waves may be assumed to be equal to the sum of the heights from the two trains.


WAVE ABSORBER
80' R
41 42 43 44 45 46 47 48
45'
31 32 33 34 35 36 37 38
30'
21 22 23 24 25 26 27 27.5 28
20'
11 12 13 14 15 16 17 18
10'
WAVE ABSORBER
BEACH
BREAKWATER
ORIGIN
Y
-X
WAVE ABSORBER
10'
15'
STA. "A"
WAVE SPLITTERS
121' 7"
60'
63' 8"
NOTE
NUMBERED STATIONS SHOW OBSERVATION POINTS.
WAVE GENERATOR FLAP
15'
WAVE ABSORBER
θo
ORIGIN
SERIES A
B
θo = 90°
θo
R
ORIGIN
SERIES C
D
R = 1.50'
R = 0.75'
θo = 90°
Y
INCIDENT WAVE DIRECTION
-X
θo
ORIGIN
SERIES J
θo = 135°
SERIES E θo = 5°
F θo = 10°
S θo = 20°
H θo = 45°
θo
ORIGIN

A. - LAYOUT OF WAVE BASIN

B - BREAKWATER CONDITIONS INVESTIGATED

Fig. 4--Model basin arrangement for wave-diffraction studies; A, layout of wave basin; B, breakwater conditions investigated

Experiments

In order to test the validity of the foregoing theory of water-wave diffraction by a rigid breakwater, an experimental investigation was undertaken in the Fluid Mechanics Laboratory of the University of California, Berkeley. Measurements were restricted to only those required for the diffraction coefficient and not for crest lag.

Wave-basin arrangements--The experimental arrangement is shown in Figure 4. All vertical surfaces which would cause reflection of waves were provided with wave absorbers which consisted of gradually sloping rough beaches. The arrangement shown in Figure 4A is for the breakwater aligned at 90° to the direction of incident-wave propagation ($\theta_0 = 90°$). The numbered stations represent the location of wave-height recorders for all runs. The effect of angle of wave incidence was also investigated by arranging the breakwater as shown in Figure 4B. Moreover, for $\theta_0 = 90°$, additional studies were made for a breakwater with rounded tip for two radii as shown in Figure 4B.

The depth of fresh water in the basin being restricted to 1.5 ft, the maximum wave period for deep-water conditions was 0.76 sec. The minimum period that could be used safely was governed largely by harmonics of the natural period of oscillation of the wave basin and by the stability of the waves at the instant of leaving the wave generator. Accordingly, the lowest wave period used was 0.70 sec. Only one wave period is theoretically required to check the diffraction theory. However, investigation with a second wave period served to check the first results.

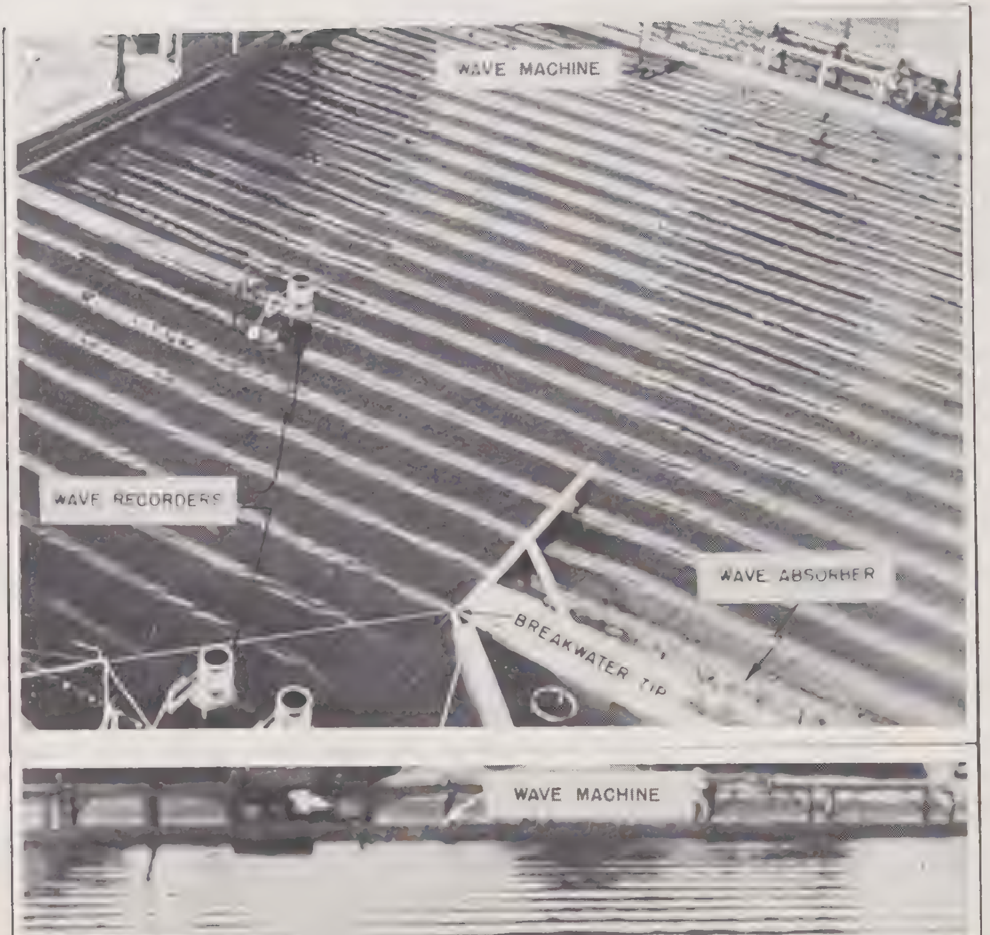

WAVE MACHINE
WAVE RECORDERS
WAVE ABSORBER
BREAKWATER TIP
WAVE MACHINE
BREAKWATER TIP

Fig. 5--Views of experimental equipment showing wave machine, wave recorders, and effect of diffraction for a breakwater at 45 degrees to the incident wave (wave period = 0.70 sec)

Waves of constant amplitude and period were generated by means of a flap which was hinged at the bottom of the basin and made to rock back and forth with a crank mechanism driven by a direct current motor.

Wave-height measurements--Wave heights were measured with float-type recorders as shown in Figure 5, which had been calibrated by direct comparison with electrical point-gage measurements of the same group of waves that was recorded on the float gages during the calibration runs. A series of carefully controlled experiments was made in order to estimate the accuracy of the wave-height measurements as influenced by accidental variations in incident-wave height, effect of small wind gusts, and instrument response. The results indicated that the wave heights were determined with a probable error of ± 12 per cent. By use of electrical resistance or capacity recording gages or pressure-sensitive recording gages and by enclosing the wave basin to avoid the effect of air disturbances, the accuracy of wave-height measurements could be improved.

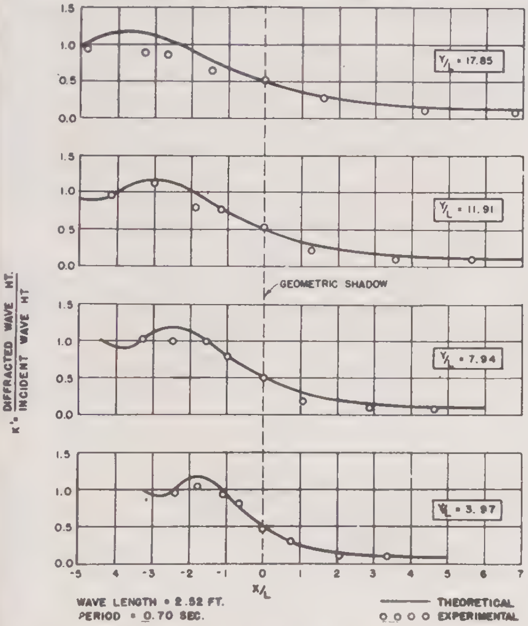


Fig. 6--Diffraction coefficients with breakwater at 90° to incident waves

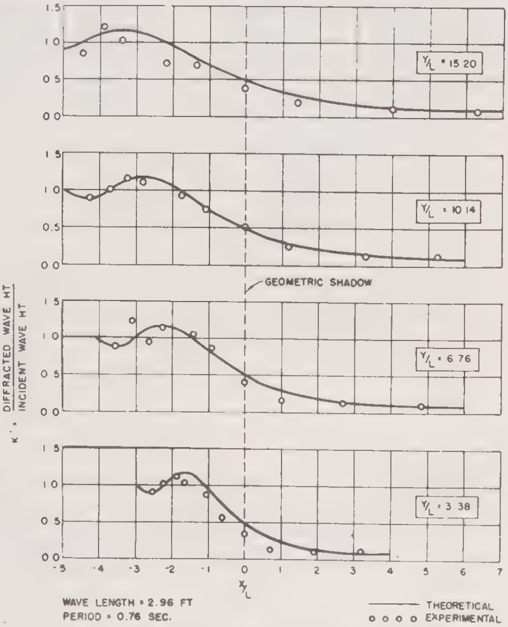


Fig. 7--Diffraction coefficients with breakwater at 90° to incident waves

Experimental procedure--Six wave-height recorders were available for the studies. For each run, one wave recorder always was operated at Station A (see Figs. 4 and 5) in order to obtain the height of the incident waves. The other five recorders were operated at selected stations in the lee of the breakwater. Approximately four runs were made for each set of five stations until the entire area beyond the breakwater had been covered. Wave periods were obtained by counting strokes of the wave generator during one-minute intervals at the beginning and end of each run. Wave periods could be reproduced very easily with probable errors less than one-tenth per cent. The average value of the ratio of wave height to wave length in deep water was approximately equal to 0.035 which closely approximates waves of small amplitude.

Experimental results--The averaged experimental results are plotted in Figures 6 to 11 covering the entire range of experiments. Theoretical curves based on the simplified solution expressed by (16) and (17) are also shown. The breakwater tip is at the origin of coordinates and extends in the positive x-direction. The quantity used for comparison is the diffraction factor K' = diffracted wave height/incident wave height.

Comparison of experiment with theory

The diffraction theory is applicable to all angles of incidence and wave periods but is not intended to apply to other than sharp-cornered breakwater tips. The theory also assumes a semi-infinite breakwater of negligible thickness, and wave crests extending to infinity in both directions.

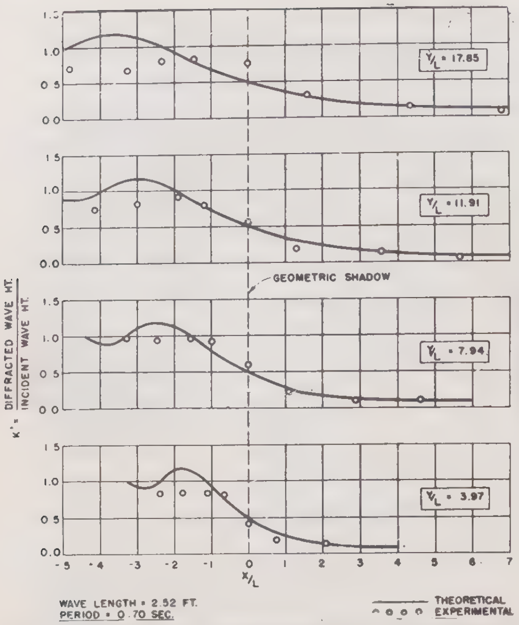


Fig. 8--Diffraction coefficients with breakwater at 45° to incident waves

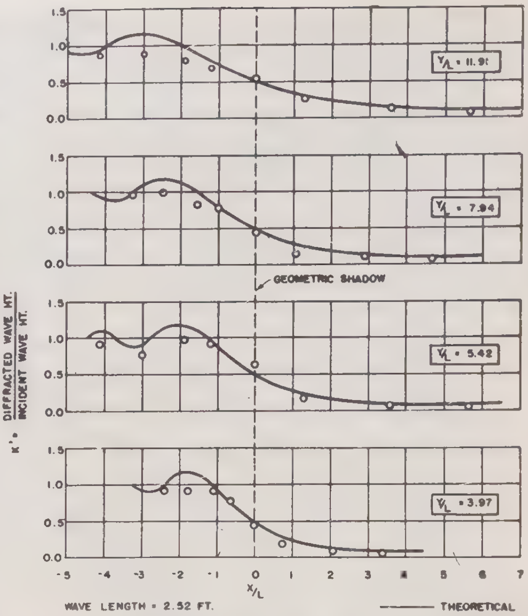


Fig. 9--Diffraction coefficients with breakwater at 135° to incident waves

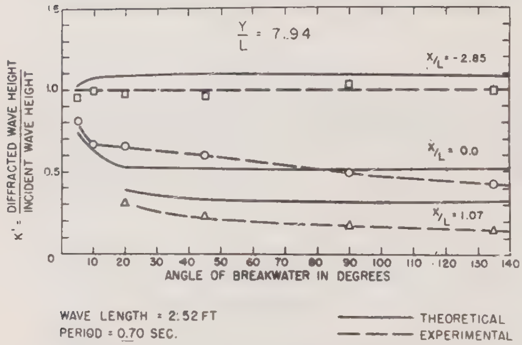


Fig. 10--Effect of angle of breakwater on the diffraction coefficient

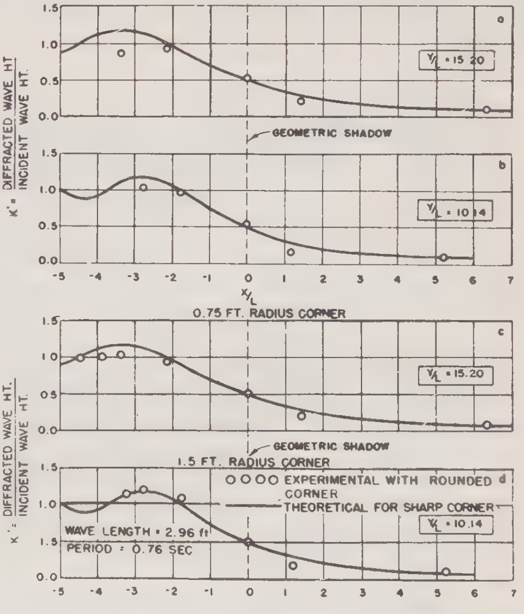


Fig. 11--Diffraction coefficients with rounded breakwater tips

Referring to Figures 6 and 7, it can be seen that wave period had little effect on the diffraction behavior. In general, the agreement with the simplified solution is remarkably good in the lee of the breakwater, even for short distances to leeward where it might be expected that the complete solution should give better agreement. Inspection of Figure 3 indicates that the complete solution for $y/L = 3.97$ yields values of K′ somewhat in excess of both the simplified solution and the experimental values. The nature of the term omitted in the derivation of the simplified solution is such that the difference between the complete and simplified solutions increases from approximately zero at $y/L = 10$ to a maximum at $y/L = 0$. The agreement of the experimental results with the simplified solution, rather than with the complete solution, may be due to the finite thickness of the experimental breakwater. However, this explanation cannot be definitely established since there are not sufficient experimental data for smaller values of y/L. In the unprotected region, outside the geometric shadow, larger differences occur between experiment and theory. The actual wave heights are generally smaller than heights predicted by theory although the deviations are within the order of magnitude of the experimental errors. If the theoretical diffraction curves were to be used for breakwater-design purposes, results would be conservative in that the actual wave heights would tend to be somewhat less than predicted values.

The results presented in Figures 8 and 9 are for waves of period 0.70 sec period and for breakwater directions of 45° and 135°, respectively. Again the agreement between theory and experiment is reasonably good in the protected region. However, in the unprotected region the difference becomes quite large, with the experimental wave heights generally being considerably smaller than the theoretical heights. In these two figures the breakwater tip is at the origin of coordinates, but the breakwater itself extends toward the right of the geometric shadow and at the appropriate angle.

Values of K′ have been plotted against breakwater angle for various values of x/L and a value of y/L = 7.94 in Figure 10. Comparison is made with theoretical values based, in this case, on the complete solution. For x/L = -2.85 (outside the geometric shadow) the diffraction coefficients obtained experimentally are approximately 18 per cent less than the theoretical value of K′ = 1.18. At the geometric shadow (x/L = 0) the experimental value agrees with the theoretical value of a breakwater angle of 90°. With increasing breakwater angle the experimental values are less than the theoretical values. For angles less than 90° the experimental values are larger than the theoretical, reaching a maximum deviation at 20°. The same behavior occurs in the lee of the breakwater (x/L = 1.07) except that the experimental results all fall below the theoretical values.

The results presented in Figure 11 were obtained for breakwater tips with rounded ends. Evidently the geometrical shape of the breakwater tip, within the limits of this investigation, has no material influence on the wave-diffraction pattern. With the sharp corner it was observed that a secondary disturbance originated at the corner which propagated capillary waves with a circular pattern superposed upon the main gravity-wave system. Rounding of the corners eliminated all such secondary capillary-wave systems. The finite thickness of the breakwater may account for many of the discrepancies between the observed diffraction behavior and the theoretical behavior which assumes a breakwater of negligible thickness.

In this investigation no attempt was made to compare theoretical crest lags with experimental values. Crest lag is of secondary importance in most harbor design. However, it is of importance where beach erosion may take place on enclosed beaches as at Long Beach, California, or on sea-coast beaches in the lee of offshore islands or projecting headlands. In this connection, crest lag becomes of importance in determining wave direction and refraction diagrams. Experiments currently underway in the Fluid Mechanics Laboratory include measurements of crest lag in connection with an investigation of diffraction by gaps in breakwaters.

Conclusions

Although the accuracy with which the diffraction coefficients could be determined experimentally is not all that might be desired, it is possible to make the following conclusions:

(1) The experimental results verify the general form of the wave-diffraction theory.

(2) Best agreement was obtained for the region sheltered by the breakwater for all angles of incidence investigated. In the region close behind the breakwater the experimental values agree almost perfectly with the simplified theoretical solution. The complete solution yields diffraction coefficients in this region which are too large compared to the experimental values.

(3) At increasing values of y/L the simplified solution approaches the complete solution so that the former, which is less complicated, may be applied safely for all values of y/L.

(4) Outside the geometric shadow the experimental wave heights were, in general, considerably less than the theoretical heights.

(5) In all cases investigated the effect of wave period was negligible.

(6) Within the limits of the experimental conditions no effect on diffraction resulted from rounding off the tip of the breakwater.

(7) The simplified theoretical solution may be applied to the location and design of breakwaters with conservative results. In other words, the predicted wave heights in disturbed regions in the lee of the breakwater will be somewhat larger than the height of waves that may be expected in nature.

Acknowledgments--This work represents results of research carried out for the Hydrographic Office, the Office of Naval Research, the Bureau of Yards and Docks, and the Bureau of Ships of the Navy Department under contract with the University of California.

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Forecasting Hawaiian Swell from January 2 to 5, 1947 [1]

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ABSTRACT

The adequacy of existing forecasting techniques is demonstrated for a situation involving extreme wave conditions on the northern shores of the Hawaiian Islands. Computations of wave characteristics as made from Sverdrup and Munk's revised relationships show that this unusually high swell could be forecast more than 24 hours in advance. Travel time is computed on the basis of the group velocity at the end of the decay distance. The situation affords a particularly good check on computed travel time since the time of maximum wave height is observed at both the Hawaiian and Palmyra Islands.

INTRODUCTION

WAVES BETWEEN 20 and 40 feet high crashing against the northern shores of the Hawaiian Islands from January 2 to 5, 1947, caused damage estimated at between one and two million dollars. The breakwaters at Kahului Harbor, Maui, alone sustained damage totaling one-half million dollars. Lives were threatened when waves overturned a sea wall near Hilo and water rushed into the Puu Maile Hospital.

These large waves were produced by high winds more than 500 miles north of the islands. Unlike the tsunami (tidal wave) which caused so much damage eight months earlier, their occurrence and characteristics could be forecast more than 24 hours in advance. Such forecasting offers an important peacetime application for the methods developed during the war by Sverdrup and Munk [1946 a, b; 1947].

The purpose of the present report is to demonstrate that since even such extreme wave conditions are entirely due to wind, they can be forecast using techniques already in existence. The deep water characteristics of the swell can be obtained from nothing more than synoptic weather maps and forecasting graphs. For breaker characteristics a refraction diagram is usually necesary in order to determine the effect of bottom topography. Kahului Harbor is used as an example.

COMPUTATIONS FROM WEATHER MAPS

The swell was produced by the northerly winds associated with a deep low-pressure center which remained approximately stationary 1,000 miles northeast of the Hawaiian Islands from January 1–4. Representative weather maps are reproduced in FIGURE 1 with fetch areas shaded. The winds obtained from the 6-hourly weather

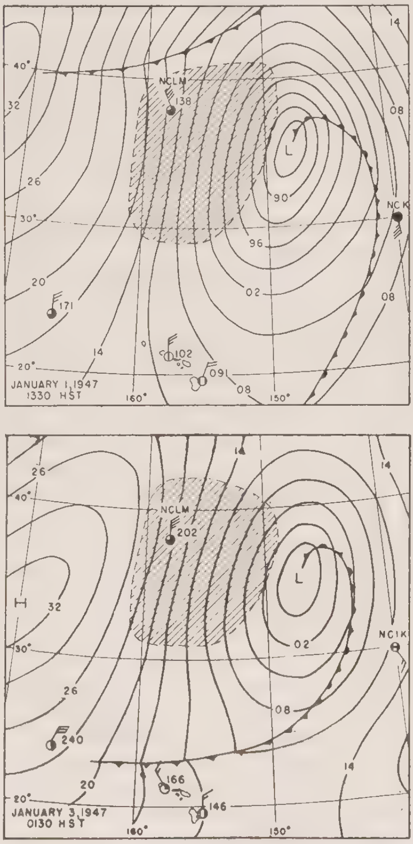

FIGURE 1. Weather maps for 1330 Hawaiian Standard Time, January 1, 1947 and 0130 Hawaiian Standard Time, January 3, 1947. The shaded areas represent the fetches.

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 372. This work represents results of research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the Navy Department under contract with the University of California.

TABLE 1.—WIND REPORTED FROM PATROL SHIP NEAR 38°N–158°W

Time	Direction	Velocity	
		Beaufort	Knots
31–1330*	NE	5	17–21
31–1930	NNW	5	17–21
1–0130	NNW	7	28–33
1–0730	N	9	41–47
1–1330	NNW	8	34–40
1–1930	NNW	8	34–40
2–0130	NNW	9	41–47
2–0730	N	8	34–40
2–1330	N	8	34–40
2–1930	N	10	48–55
3–0130	N	7	28–33
3–0730	NNW	8	34–40
3–1330	NNW	6	22–27
3–1930	NNE	6	22–27
4–0130	NNE	5	17–21
4–0730	NNE	6	22–27
4–1330	N	6	22–27

* December 31, 1946, 1330 Hawaiian Standard Time.

reports made by the patrol ship in the area are listed in TABLE 1.

The wave characteristics given in TABLE 2 have been computed by use of the forecasting technique explained in *Wind Waves and Swell—Principles in Forecasting* [Hydrographic Office, 1943] and *Breakers and Surf—Principles in Forecasting* [Hydrographic Office, 1944]. The forecasting graphs used, however, are those based on the revisions given by Sverdrup and Munk [1946 a, b; 1947] except that the travel time has been computed on the basis of the group velocity of the swell at the end of the decay distance.

Such a relationship for travel time was first suggested in 1944 by Robert Stump, formerly Captain, Army Air Forces, who at that time was engaged in wave research and forecasting at the United States Navy Weather Central, San Francisco, and the University of California, Fluid Mechanics Laboratory, Berkeley. Munk [1947] and Sverdrup [1947] investigated swell from the standpoint of impulsively generated waves, and developed a theoretical basis for the new method of computing travel time which will be incorporated in revised forecasting graphs. N. F. Barber and F. Ursell [1947] of the Admiralty Research Laboratory, Teddington, England, also verified the correctness of the new relationship.

Stump checked travel times during a two-year period of daily wave forecasts and obtained consistently better results with the proposed relationship. The present situation offers the unusual opportunity of checking travel times at two widely separated points along the decay path. The correctness of the proposed relationship as compared to the original relationship will be demonstrated.

The deep-water swell characteristics listed in TABLE 2 were computed specifically for Kahului Harbor, Maui, but they would apply with only slight modification to other nearby islands in the Hawaiian Group. Characteristics of the highest waves reaching Palmyra Island (6°N–162°W) are also given.

The fetch locations show that the swell would approach Kahului Harbor from directions between N10°W and N15°E. FIGURE 2 is a part of the refraction diagram for a 14 second period and N10°E direction at Kahului Harbor. The period corresponds to the period of the highest swell. The direction chosen is that which within the variability of direction would appear to give the greatest concentration of wave energy at the harbor. The complete diagram from which FIGURE 2 is taken was drawn with a crest interval of one-half the wave period on a detailed chart of the bottom topography.

The diagram shows a complex wave pattern caused by the off-shore ridge. A similar crossing of wave trains has been observed north of Scripps Canyon, La Jolla, and the various features have been discussed by Munk and Traylor [1947]. In order to show the degree of convergence or divergence for the portions of the wave crests reaching the harbor, the width of the crest lines has been drawn proportional to the refraction factor K, according to the scale in the legend. The refraction factors

TABLE 2.—WAVE COMPUTATIONS FOR HAWAIIAN AND PALMYRA ISLANDS

Position	Kahului Harbor, Maui						Palmyra (Highest Waves Only)
Map Time	1–0130	1–1330	2–0130	2–1930	3–0730	3–1330	2–1930
Average wind velocity,* U (knots)	28	34	41	45	34	27	45
Fetch, F (naut. miles)	700	700	700	700	700	700	700
Duration of wind, t_d (hours)	16	20	21	32	00	00	32
Minimum duration, t_{min} (hours)	60	55	50	48	55	60	48
Wave height at end of fetch, H_F (feet)	14	21	28	38	25	15	38
Wave period at end of fetch, T_F (seconds)	6.5	8.0	9.1	11.3	11.7	10.1	11.3
Distance of decay, D (naut. miles)	500	500	500	600	660	660	1500
Reduction factor for height, H_D/H_F	0.33	0.45	0.51	0.58	0.57	0.50	0.33
Height at end of decay, H_D (feet)	4.6	9.5	14.3	22.0	14.2	7.5	12.5
Period at end of decay, T_D (seconds)	9.9	10.9	11.5	14.0	14.5	13.2	17.1
Travel time, t_D (hours)	33	30	28	28	30	33	57
Computed Arrival Time	2–1030	2–1930	3–0530	3–2330	4–1330	4–2230	5–0430
Refraction factor, K	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Depth of breaking, d_b (feet)	8.8	15.8	22.2	33.8	24.7	14.7	24.5
Breaker height, H_b (feet)	6.9	12.3	17.3	26.4	19.3	11.5	19.1

* Notation is that of *H. O. Misc. 11,275* and *H. O. 234*.

in the most shallow water have been computed from the modified formula for breakers given by Munk and Traylor.

The refraction factors for the breakers reaching the harbor vary between 0.3 and 1.2. Results would be somewhat modified for the shorter period swell which arrives earlier. Breaker heights have been computed for $K = 1.0$ and listed in TABLE 2. Because of interference between wave trains and differences in the refraction factor, the highest breakers at certain places along the breakwater may be expected to be as much as 50% higher than those tabulated.

OBSERVATIONS AND DAMAGE

Reports from various islands in the Hawaiian group indicate that breakers 20 to 40 feet high were observed at many places. No observations of wave period are available. Highway washouts and severe shore erosion were general along the exposed northern shores of all islands.

The damaged sections of the breakwaters at Kahului Harbor are shown in FIGURE 2. Curves representing the computed breaker height and swell height as functions of time are given in FIGURE 3. The observational data are taken from reports compiled by William Walsh, manager of the Kahului Railroad Company. These reports show that the highest waves reached Kahului between 2300 HST, January 3 and 0200 HST, January 4, which compares favorably with the computed time of 2330 HST, January 3.

On the island of Hawaii, the Laupahoe-

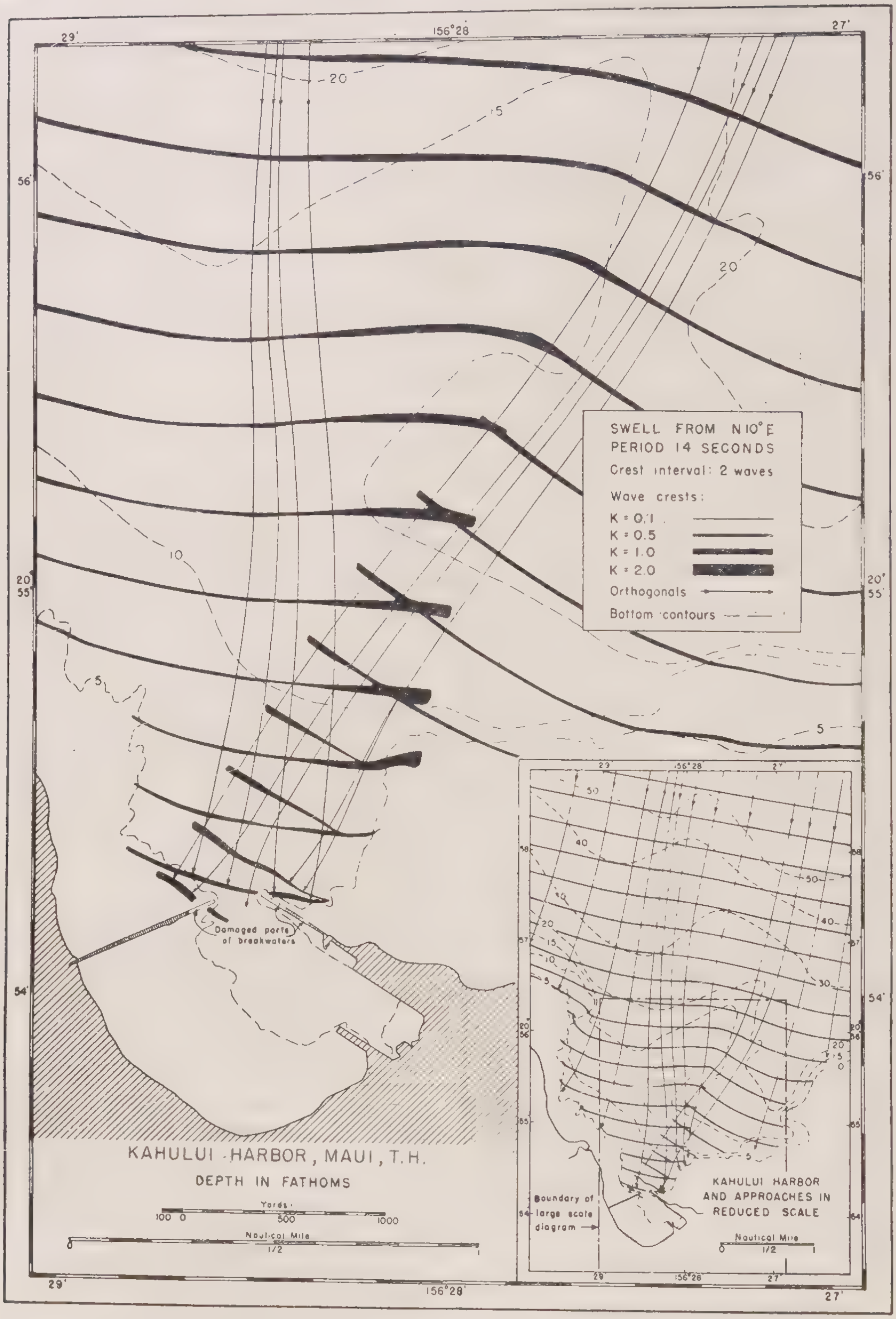
29'
156°28'
27'
56'
20° 55'
54'
20
15
10
5
SWELL FROM N10°E
PERIOD 14 SECONDS
Crest interval: 2 waves
Wave crests:
K = 0.1
K = 0.5
K = 1.0
K = 2.0
Orthogonals
Bottom contours
Damaged parts of breakwaters
KAHULUI HARBOR, MAUI, T.H.
DEPTH IN FATHOMS
Yards
100 0 500 1000
Nautical Mile
0 1/2 1
50
40
30
Boundary of large scale diagram
KAHULUI HARBOR AND APPROACHES IN REDUCED SCALE
Nautical Mile
0 1/2

FIGURE 2. Refraction diagram for Kahului Harbor, Maui, T. H. Damaged parts of breakwaters are unshaded. The degree of convergence and divergence is indicated on the large-scale diagram by the width of the wave crest lines.

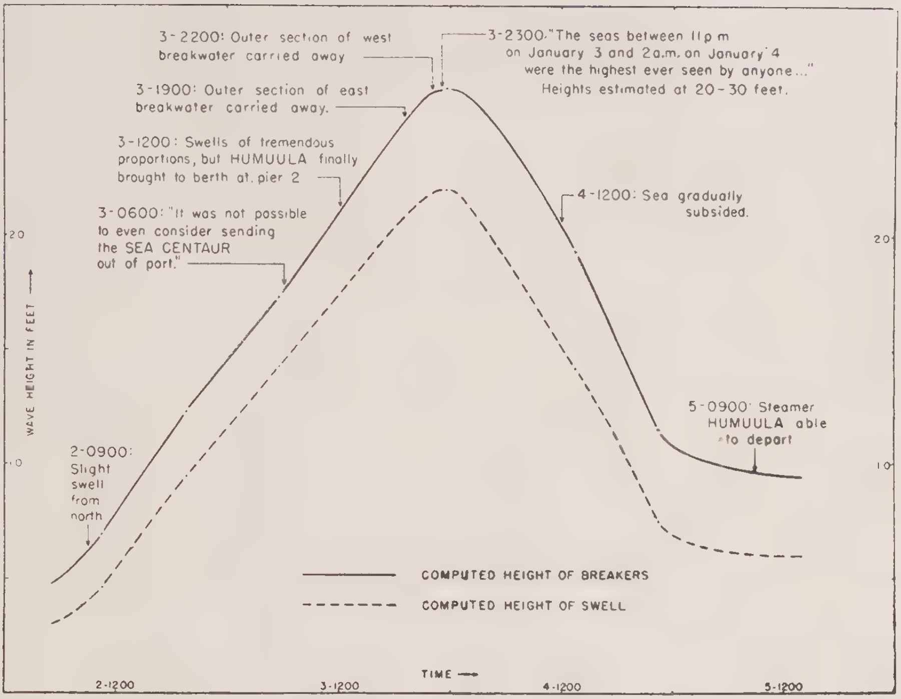

FIGURE 3. Computed swell and breaker heights as a function of computed date and hour of arrival. Observational data is shown for comparison.

hoe Lighthouse was knocked from its foundation by 20 to 30-foot waves. It is of importance to note that this lighthouse withstood the tsunami of April 1, 1946 when a 30 foot rise was reported [MacDonald, Shepard, and Cox, 1947].

Three waves are reported to have swept over low-lying Cooper Island in the Palmyra Atoll. The highest surf occurred between 0300 and 0600 HST on January 5, and the computed arrival time is 0430 HST, January 5. Swell just beyond the reef was estimated as 20 feet high, but much of the wave energy was dissipated on the reef.

CONCLUSIONS

The computed wave heights agree with such observations as are available, and the adequacy of existing forecasting techniques for this situation is demonstrated. The computed arrival times of the highest waves at both the Hawaiian and Palmyra Islands compare remarkably well with observed times. The arrival time at Palmyra, if it had been computed by the original relationship, would be 12 hours later than the observed arrival time. Since such a large discrepancy could hardly be due to the manner in which the forecasting techniques were applied, the correctness of the revised travel time relationship mentioned above is demonstrated.

ACKNOWLEDGMENTS

Dr. Richard H. Fleming of the Hydrographic Office and Captain H. T. Orville, USN, of the Office of the Chief of Naval Operations, United States Navy, have furnished the weather and wave data which have made this study possible.

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Acoustical Characteristics of Noise Produced by Snapping Shrimp*

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ome marine animals produce sounds which, under cer- conditions, completely dominate the ambient noise in sea. The snapping shrimp (not to be confused with the le shrimp) are the most widely distributed of these mals; they are frequently less than 3 cm in length and luces the sound by snapping of the claw. Shrimp noise is y to be found around the world in tropical and sub- ical waters less than 55 meters deep wherever rock, l, or other material on the bottom provides interstices hich shrimp thrive. This paper describing the acoustic put of the snapping shrimp (*Crangon* and *Synalpheus*) ased upon measurements made off the Southwestern Southeastern coasts of the United States, the Hawaiian nds, and several islands in the Southwest Pacific. Over rimp bed, the noise spectrum is found to be roughly pendent of frequency from 2 to 24 kc (the upper limit of measurement), whereas the ambient noise normally present in the deep sea decreases with frequency. There is a broad peak in the shrimp spectrum somewhere between 2 and 15 kc. Over a shrimp bed the noise at 20 kc is about 25 db above the ambient noise which accompanies a sea state of 2 (waves less than a meter high, not including swell). For low sea states, shrimp noise is appreciable a mile or more from the boundary of the bed. The maximum diurnal variation of shrimp noise is from 3 to 6 db, the noise being greater at night. Single snaps from isolated specimens have been subjected to a Fourier integral analysis which indicates a spectrum comparable to that measured over shrimp beds where the underwater sound consists of a multitude of snaps. A typical peak sound pressure at the distance of a meter from a single shrimp is of the order of 200 dynes/cm².

INTRODUCTION

HE interest focused upon devices utilizing the propagation of sound in the sea during past six years has materially enlarged our s of the truly amazing sounds produced by ine animals, both vertebrate and invertebrate, ing special organs capable of generating nds.[1,2] Thus, the so-called "silent deep" takes a renewed interest not only for the marine logist, but for the physicist as well.

f all these sounds produced by animals in the , including incidental sounds such as the nching of shells in eating or sounds associated with locomotion, none exceeds in importance the steady, day-in, day-out, year-around crackling from populations of snapping shrimp. Moreover, the geographical distribution of underwater noise produced by these crustaceans is not exceeded by that of any other known marine animals.

The sharp snap produced individually by these animals has long been known to biologists, but has not been suspected of being a major source of underwater sound. The snaps of a few shrimp in a small vessel of water may be heard clearly across a room. Under quiet conditions the crackling noise of a population of these crustaceans may be heard by the unaided ear above the water surface despite the very large loss in sound transmission across the water-air boundary; the crisp, frying noise produced by the shrimp may be readily heard by swimmers upon submerging their ears.

Of the many genera of "snapping shrimp," only the species of two genera, *Crangon* and *Synalpheus*, are capable of vigorous snapping. Figure 1 is a photograph of *Crangon californiensis*

The work forming the basis of this report was done er contracts OEMsr-30 and NObs-2074, respectively, the Office of Scientific Research and Development ction 6.1 NDRC) and the Bureau of Ships, Navy artment, while the authors were members of the staff of University of California Division of War Research at U. S. Navy Radio and Sound Laboratory (now called U. S. Navy Electronics Laboratory), San Diego, fornia.

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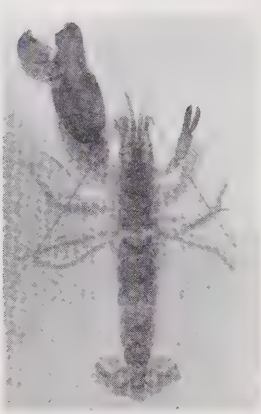

FIG. 1. Photograph of the snapping shrimp *Crangon califoriensis* (natural size) (from Johnson, Everest, and Young).

which is usually less than 4 cm long. This is one of several species which are acoustically active along the California coast. Most prominent among other species are *Synalpheus lockingtoni* and *Crangon clamator* (called *Crangon dentipes* in many California biological reports including reference 3). The snapping shrimp should not be confused with the common edible shrimp which is usually larger and produces no noise.

Biological studies indicate that the snapping shrimp live mainly where the water temperature for the greater part of the year is warmer than 11°C to depths of about 55 meters and on bottoms composed of rock, shell, coral, or other sheltering materials. Consequently, the shrimp are to be found extensively in the tropical and sub-tropical coastal waters throughout the world.

This paper is intended to cover primarily the acoustical characteristics gleaned from extensive observations that have been made upon the crackling noise caused by the snapping shrimp. The biological aspects governing the production, maintenance, and geographical distribution of the noise are dealt with in a complementary report.[3]

SCOPE OF MEASUREMENTS

Early in 1942 an investigation of underwater ambient noise was started in the vicinity of San Diego. From the beginning of field tests a characteristic crackling noise of great magnitude wa
observed off Point Loma, in the San Diego Yach
Harbor, and soon after in the waters off La Joll
Oceanside, the Los Coronados Islands, and othe
places off the Southern California coast. Th
source of the noise was shrouded in mystery fo
many months, but the possibility of its being
biological origin led to a special investigatio
along this line. Meanwhile, considerable progre
was made in determining the acoustical spectru
and in establishing the presence of the cracklin
noise in local coastal waters over rock bottom
around piers, and in harbors. In December 194
the crackling sound was conclusively demo
strated to originate in the claw-snapping activ
ties of snapping shrimp.

Between 1942 and 1944 the shrimp noi
spectrum was measured along the Southeaste
Coast[4] of the United States (Florida, Bahamas
the Southwestern Coast of the United Stat
(San Diego), in the Central Pacific Area (H
waiian group including Midway), and in t
Southwestern Pacific Area[5] (Funafuti, Noume
Russell Islands, and Guadalcanal). In addition
these four general areas, at several score oth
localities qualitative listening observations we

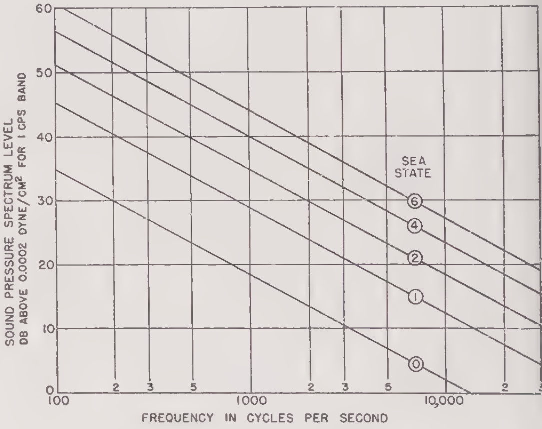

FIG. 2. Average ambient noise spectra in deep water
absence of shrimp noise, showing influence of state
sea.

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[3] M. W. Johnson, F. A. Everest, and R. W. Young, "The role of snapping shrimp (*Crangon* and *Synalpheus*) in the production of underwater noise in the sea," Biological Bulletin **93**, 122–138 (1947).

[4] Most of these observations were made in cooperati
with the Columbia University Division of War Researc
the Bureau of Ordnance, and the Naval Ordnance Lal
ratory.

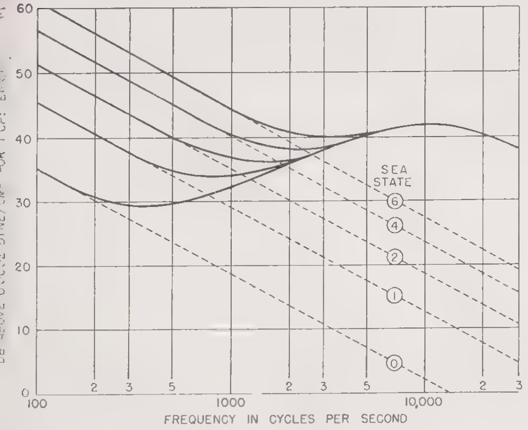
[5] These field data and part of those in the Central Pac
were collected by W. E. Loomis of the Naval Ordna
Laboratory during a survey in cooperation with t
organization.

de, such as along the Northwestern Coast of United States and at Bikini in 1946.

EQUIPMENT

rdinarily the non-directional hydrophone (of piezoelectric type, utilizing x cut Rochelle or *ADP* crystals) was suspended at half the er depth but not deeper than 15 meters. The ctrum analyzing system for very portable rations usually included an adjustable octave half-octave filter, and a battery-operated, nd level indicating meter. When weight limi- ons would allow, an a.c.-operated, narrow- d (e.g., 50 c.p.s.) heterodyne frequency ana- er or similar device was utilized to feed a phic level recorder. Installations for continu- observations of the wide-band noise consisted hydrophone mounted on a tripod on the sea tom, an amplifier-rectifier, and clock-driven ording milliammeter. This system had its ncipal sensitivity from 1 to 10 kc.

alibration of all parts of the system was made frequent intervals; hydrophone calibrations e not always consistent. Some hydrophones jected to the same kind of single frequency ne wave calibration were found to differ in r response to shrimp crackle. The calibrations Rochelle salt hydrophones changed appreci- in tropical waters where temperatures are ve the Curie point of the piezoelectric ma- al. At times, considerable effort was required scape interfering noises originating on the carrying the measuring equipment or re- ng from motion of the hydrophone through the water. Correction was applied whenever necessary to yield random incidence response.



3. Idealized underwater ambient noise spectra over shrimp bed, for various sea states.

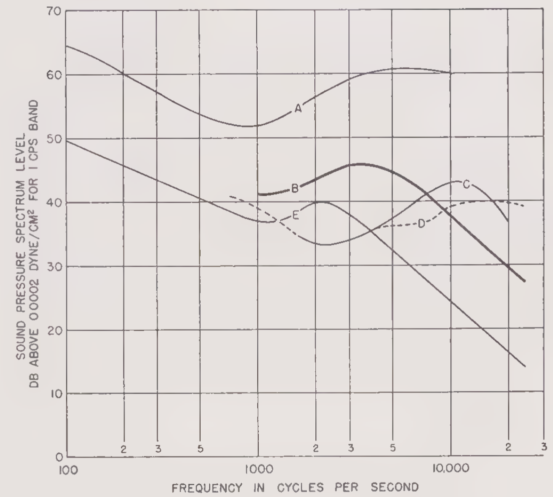


FIG. 4. Shrimp noise spectra from different parts of the world:

A. Kaneohe Bay, Oahu (Hawaiian Islands),
B. Off Point Loma (San Diego, California),
C. Florida-Bahamas,
D. Southwest Pacific, and
E. San Diego Yacht Harbor.

The results given below are largely in the frequency range 0.1 to 24 kc. Although the observations were made with filters whose pass bands ranged from 50 c.p.s. to an octave at the frequency concerned, they have all been reduced to sound pressure spectrum level upon the assumption of uniform energy distribution within these bands. The spectrum level is the r.m.s. pressure level associated with that sound energy contained in a band one cycle per second wide centered at the frequency indicated. The r.m.s. reference pressure in this paper is 0.0002 dyne/cm².

AMBIENT NOISE OVER SHRIMP BEDS

In order to show what part of underwater ambient noise is caused by snapping shrimp, it is first appropriate to consider the ambient noise in the deep sea where both man-made noises and sounds of biological origin are absent. Such ambient noise decreases regularly with frequency as indicated by the parallel lines in Fig. 2. These curves are taken from a survey[6] of the deep sea ambient noise as measured by many observers

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[6] Some of the results of this survey by V. O. Knudsen, R. S. Alford, and J. W. Emling are to appear soon in the J. Marine Research, Vol. **7**, No. 3, in an article by those authors entitled, "Underwater ambient noise."

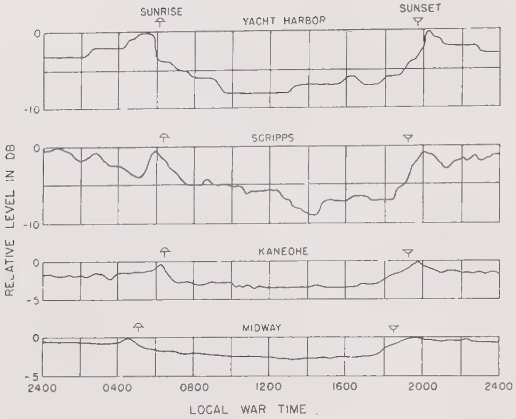

FIG. 5. Diurnal change in wide band shrimp noise at four locations: San Diego Yacht Harbor, 7 August 1942, Scripps Institution of Oceanography, 21 August 1942, Kaneohe Bay, Island of Oahu, 19–20 April 1943, and Midway Island, 2 June 1943.

under widely different conditions. Since this noise appears to be something inherent in the sea, it is simply referred to below as the "water noise."

The "sea state" indicated in Fig. 2 is a scale employed by marine meteorological observers[7] to represent wave heights which are, of course, related to the local winds. In a state 2 sea, for example, the waves are between 1 and 3 feet high; for a state 3 sea, the waves are estimated to be between 3 and 5 feet high. A dead calm is a state 0. The sea represents a separate water motion superimposed upon and in addition to the swell.

Shrimp crackle changes the underwater ambient noise level very markedly. The solid curves in Fig. 3 show idealized combinations of the previously described water noise spectra with shrimp noise in shallow water having a large shrimp colony. Between 2 and 20 kc, shrimp noise is nearly constant, its spectrum level being about

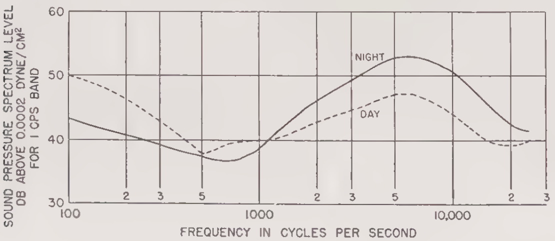

FIG. 6. Example of diurnal change in shrimp noise spectrum.

40 db above 0.0002 dyne per cm². Below about kç shrimp noise contribution is small, but gene ally above 2 kc it completely dominates wat noise. The relative importance of the two kinds noise changes, of course, with the sea state. At 1 and 20 kc shrimp crackle is about 25 db abo water noise for sea state 2. Quantitative measur ments above 24 kc are not available, but aur observations in 8-kc bands heterodyned to t audible range from frequencies as high as 50 l reveal characteristic crackling noises similar those observed in the upper sonic region.

All of the spectra given here are for noi measured with a non-directional hydrophon The noise spectrum over a shrimp bed appears be practically independent of the hydropho depth.

VARIABILITY OF SHRIMP SPECTRA

Shrimp noise from various areas consistent shows a broad peak in the spectrum somewhe above 2 kc. However, there are differences shape, as may be judged from the spectra Fig. 4. Some of the differences among curves ma well be attributed to the measuring equipme employed, particularly above 10 kc, although t shape of the spectra measured in any one ar with given equipment was reasonably consiste

Spectrum *A* in Fig. 4 is an average of two ve consistent spectra obtained with hydrophone few feet from a pier in Kaneohe Bay in the isla of Oahu. The very high sound level (some 20 d higher than the typical spectrum of Fig. 3) caused by snapping shrimp living in the fouli material on the nearby pilings; only 20 feet aw from the pier the spectrum level was 10 db low than in spectrum *A*.

From an average of measurements in 1944 21 stations over shrimp beds off Point Lom spectrum *B* was drawn. Spectrum *C* is based observations at 23 stations in the Florid Bahamas area. Comparable measurements at total of 15 stations near Funafuti, Guadalcan and Noumea (New Caledonia) were averaged obtain spectrum *D*.

Spectrum *E* is the average of 9 sets of 19 observations in San Diego Yacht Harbor. A though shrimp crackle was prominent at th location, the spectrum is quite different in sha from the average spectrum obtained with t e equipment off Point Loma. This difference be caused by the species of shrimp (*Crangon forniensis*) found in this harbor but not in the ide areas. Spectra *C*, *D*, and *E* are all es- ially the same below 1 kc.

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[7] *Instructions to Marine Meteorological Observers*, U. S. Weather Bureau, W. B. No. 1221, June 1941, p. 54.

DIURNAL AND SEASONAL VARIATIONS

n order to investigate possible diurnal varia- s, continuous records of shrimp noise were ained in the San Diego Yacht Harbor, at the of Scripps Institution of Oceanography at Jolla, in Kaneohe Bay, and at Midway Island. may be seen from the examples in Fig. 5, the eme variation in the wide band noise was re than 6 db at the first two locations and ut 3 db at the other two. The times at which rise and sunset occurred at each location are icated by appropriate symbols in the figure. parently increased activity of the shrimp rtly before sunrise and after sunset results in ht peaks at these times.

he nature of the diurnal change in spectrum be judged from curves in Fig. 6, obtained at pier at Scripps Institution of Oceanography 4–5 April 1944. The solid curve represents the age of 11 nocturnal spectra measured at s between 1920 and 0656. The dashed curve he average of 6 spectra taken from 0747 to on 5 April 1944. Note that the broad peak e neighborhood of 5 kc is 6 db higher at night during the day. It is believed that the rise in ow frequency end of the spectrum during the is to be attributed to sources other than the ping shrimp.

bservations made so far have disclosed no eciable seasonal variation in shrimp noise. s condition may not apply near boundaries of shrimp belt or in other places having large sonal variations in water temperatures.

DEPENDENCE OF NOISE SPECTRUM ON DISTANCE FROM SHRIMP BED

s snapping shrimp colonies exist only where depth of water and bottom types are suitable, shrimp thus constitute a source distributed er beds which are localized to greater or less ent. As would be expected from the habits of shrimp, the noise level remains essentially stant over a shrimp bed, and decreases with tance from the edge of the bed. Note that the situation differs somewhat from the more usual transmission problem which considers a concentrated sound source.

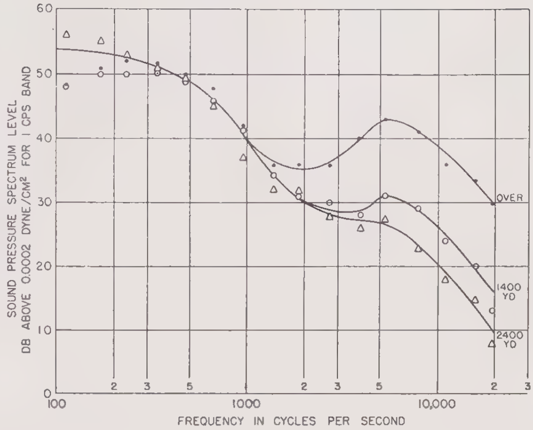

FIG. 7. Spectra of shrimp noise over and at two distances from edge of shrimp bed.

Figure 7 illustrates the change in noise spectrum with distance from the edge of a shrimp bed; the spectrum over the bed is included for comparison. The location is six miles south of Point Loma. The distances shown in the figure are measured toward open sea and deep water from the edge of a patch of cobbles which afford cover for the shrimp. This region was selected for a rather intensive study because a relatively great amount of information is available[8] about bottom types here. Some idea of the spread of single observations may be seen from the plotted points, since these are *not* averages as elsewhere in this paper. As the distance increased, the measured spectrum

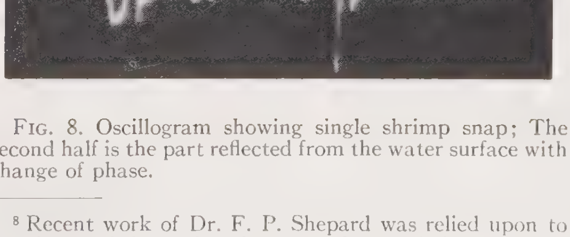

FIG. 8. Oscillogram showing single shrimp snap; The second half is the part reflected from the water surface with change of phase.

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[8] Recent work of Dr. F. P. Shepard was relied upon to supplement information shown on the usual charts.

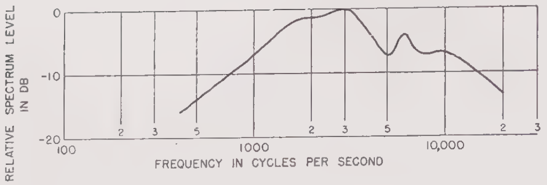

FIG. 9. Spectrum of single shrimp snap, directly transmitted.

approached that of usual ambient noise to be expected (cf. Fig. 3) for the state 2 sea of that particular day. From numerous observations of which those in Fig. 7 are reasonably typical, it may be concluded that the shrimp noise makes a measurable contribution to the total ambient noise to a distance of a mile; under very calm conditions it is appreciable for two miles.

SINGLE SHRIMP SNAPS

Shrimp noise over a bed is a continuous fusillade of snaps from individual shrimps resulting in a characteristic crackling sound. If the hydrophone is nearer to one region of a shrimp population than others contributing to the general noise level, occasional discrete loud "snaps" or "cracks" stand out, resembling the sound of burning twigs. Observations of the wave shape of individual shrimp snaps have been recorded by means of a cathode-ray oscilloscope and a high speed, moving film camera. A highly damped, wide range hydrophone picked up the signal to be fed to a linear amplifier, the over-all system response being essentially flat between 2 and 50 kc.

In a series of controlled observations in Sweetwater Lake on the snaps from individual *Crangon* and *Synalpheus* shrimp, it was found that the typical peak pressure corrected to a distance of one meter was about 200 dynes/cm^2. Impulses recorded at Scripps pier in La Jolla showed occasional peak pressures of 1000 dynes/cm^2 from shrimp on nearby piling, the distance being of the order of one meter, but uncertain.

An attempt was made to identify the shrimp from an examination of the wave form of individual snaps. While some generic differences of wave shape were tentatively observed between *Crangon* and *Synalpheus* impulses, sufficient observations have not been made to determine the plausibility of making dependable biological identifications by this method.

A typical oscillogram of an individual shrimp snap is given in Fig. 8. This was obtained at the U. S. Navy Electronics Laboratory pier in San Diego Bay, so the source is probably the common bay shrimp (*Crangon californiensis*). The first half of the oscillogram represents sound pressure transmitted directly through the water from the shrimp to the hydrophone, the second half the sound reflected from the water surface. Note that the surface-reflected component is of smaller amplitude and opposite phase than the direct. The time scale may be judged from the fact that 1.5 milliseconds elapsed between the principal positive and negative peaks. This time delay is, of course, dependent on the geometry of the experiment.

Sixteen such oscillograms were sent to the Case School of Applied Science where they were subjected to Fourier integral analysis.[9] An example of the spectrum so obtained is given in Fig. 9. This is for the direct component (the first half) of the snap shown in Fig. 8. The general shape of this spectrum is comparable to the spectra given in Fig. 4, indicating that the sound over a shrimp bed is essentially a superposition of a large number of similar individual snaps.

ACKNOWLEDGMENTS

To the score or more members of the Listening Section of the University of California Division of War Research who have contributed directly to the results reported here, the authors wish to express their appreciation. Special mention should be made of the work of G. P. Welch, T. McMillian, C. S. Manning, and R. S. Gales in the observations at sea and in data reduction. L. W. Sepmeyer made significant contributions in instrumentation. To T. F. Johnston is due much of the credit for the observations of discrete shrimp snaps and the analysis of their spectrum. To a host of others, both civilians and Naval personnel in widely separated parts of the world who have rendered material assistance and encouragement, the authors acknowledge their gratitude.

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[9] R. S. Shankland, "The analysis of pulses by means of the harmonic analyzer," J. Acous. Soc. Am. **12**, 383–386 (1941).

SEX RATIO

by WESLEY R. COE

SEX RATIO. The hereditary sexual mechanism (*see* Sex) provides that, as a general rule in animals with well-differentiated sexes, there shall be approximately equal numbers of males and females. But even in man and other mammals the ratios are not exactly equal, and in some of the lower vertebrates and invertebrates the disparity is very great. In all races of mankind more boys than girls are born. The excess of males differs somewhat in different races, in different nationalities and in different years, but is seldom more than 107 or less than 104 males to 100 females. For all races combined, there are born an average of approximately 105.5 boys to 100 girls. (For mammals and birds, see *Livestock;* for human, see *Human, at Birth and Death.*)

W. T. Russell (1936) states that the highest ratios among whites (113 males to 100 females) are reported from Greece and Korea and the lowest (104.3) from England and Japan. The ratios are considerably lower among Negroes. The average ratio at birth, exclusive of stillbirths, in the United States from 1915–42 was about 105.6, the white ratio being computed as 106.3 and the Negro ratio was 103.3. As compared with the preceding decade, there was a tendency for the ratio to decline slightly during 1930–39. The tabulations by A. Ciocco (1938) indicate that no significant differences are found between the various states, in spite of diverse national origins of the populations and varied environmental conditions. Nor are there significant differences in the month or season of birth or the time during the sexual cycle when fertilization takes place. The ratios in Germany, the Netherlands and Italy average about 106, with slightly higher ratios in Norway and Sweden and slightly lower in France. High ratios are usually reported for Jews.

The ratios at birth, *secondary* sex ratios, differ considerably from the *primary* ratios which refer to the proportion of males at the time of conception or at the earliest period of embryonic development. In man the primary ratio must be even higher than the ratio at birth, since more males than females die during prenatal development. The sex ratio of prenatal deaths in the United States during 1926–29 is stated by Russell (1936) to range from 142.6 at the fourth to sixth month of gestation to 129.3 at the seventh to ninth month, with an average of 134.5, as compared with a ratio of 105.6 for living births during the same years.

No satisfactory explanation can yet be given for the disparity of the primary sex ratio, which is probably at least as high as 115 males to 100 females, but the following suggestions have been made: (*a*) that more male-determining than female-determining sperm are produced; (*b*) that the former have greater motility than the latter or are otherwise more likely to be successful in fertilization; (*c*) that the response of the egg to the entrance of a male-determining sperm is more likely to lead to normal embryonic development; and (*d*) that more female-determined embryos die in the earliest stages of development, or before sexual differentiation can be recognized, presumably owing to the influence of sex-linked lethal genes which affect only the homozygous (female) sex. (See *Livestock.*)

The higher mortality of males which prevails before birth continues throughout life. In the United States the mortality ratio for infants less than one year of age averages about 133 males to 100 females. At the ages of 13 to 19 years the two sexes are approximately equal in numbers and thereafter there are more women than men. Hence the life expectancy of males is always less than that of females. As a consequence of this differential mortality the ratio of males to females in the total population of a country will often be less than parity except as it may be influenced by migration. In the United States the sex ratio of the total population in 1940 was 100.6 males to 100 females; for the white race it was 101.2 to 100. Aside from the greater industrial and social hazards to which the males are commonly exposed in civilized life, this differential mortality must be ascribed to some fundamental physiological difference between the two sexes, since the same condition is found in some of the lower vertebrates and in many invertebrates.

The fact that males have a higher basal metabolism than females may make the former more susceptible to unfavourable conditions. Consequently any condition, such as impaired vitality of the mother, which tends to increase the prenatal mortality, tends to decrease the proportion of boy babies. And conversely the ratio of boys will be higher from reasonably early marriages, since prenatal deaths are relatively less frequent with young mothers than with women more than 30 years of age. For the same reason the first-born children have a slightly greater chance of being boys than those born later in the same families, but there seems to be no satisfactory proof that either the absolute age or the relative age of the father influences the sex ratio. The question as to whether there is a significant increase in the ratio of male births as a consequence of prolonged wars or other social upheavals has not yet been satisfactorily answered. Statistics indicate that a slight increase did follow World War I in all the belligerent and most of the neutral nations of Europe, but not in the United States (*see* section on *Influence of War*). It is not improbable that where an increase occurred it may have been due to conditions favourable to early marriage and the resulting low prenatal mortality.

The proportion of prenatal deaths is usually somewhat lower in rural communities than in cities, and the ratio of living male births slightly higher. The union of different racial stocks sometimes results in a high male ratio, either as the influence of hybrid vigour or the suppression of defective genes. In other hybrids the reverse is true. In certain mammals inheritable divergence in sex ratios has been demonstrated and selection for high and low sex ratios has established family lines with the corresponding characteristics. It is not improbable that human families may have similar traits.

In reptiles, fishes and many invertebrates, including insects, crustaceans and molluscs, males are usually smaller than females as well as shorter lived. In some of these a selection of either the largest or the oldest individuals in the population will contain few if any males, although there may have been equality in the primary sex ratio. In many species, including even some of those in which the male is homozygous, males throughout life are more susceptible to adverse conditions, such as deficiency of oxygen, abnormal temperature, poisons and various diseases and succumb more readily than females. In various species of reptiles and fishes there are generally about equal numbers of males and females or an excess of males when young but the proportion of males decreases with increasing age until there may be only 20 to 30, or even fewer, males to 100 females. In some species of molluscs in which each individual retains the same sex throughout life, the males die when relatively young and the population of old and large individuals consists exclusively of females.

These sexual differences in susceptibility and mortality may also be due in part to the influence of sex-linked lethal or semilethal genes which would affect principally the heterozygous (heterogametic) sex (*See* Heredity.) Such genes are known to be operative in both animals and plants. Families or races having few or none of these genes would be expected to have a high ratio of males. Colour blindness and defective blood-clotting (haemophilia) are the two best-known sex-linked defects in man.

A good example of the influence of such lethal genes may be found in the fly *Drosophila melanogaster.* In this fly, which has a normal sex ratio of about 98 males to 100 females, certain genetic strains have been obtained whereby it is possible to arrange matings which will produce 66⅔%, 87½% or 100% female progeny, since one-half, three-fourths or all the males die before or soon after hatching. In other stocks the ratios may be highly variable. Another strain carries a sex-limited lethal gene and produces only males.

In a considerable number of invertebrates, in a few fishes and in certain plants, the sexuality changes during the individual's lifetime. Such individuals are usually, but not invariably, protandric, functioning as male when young and later changing to the opposite phase of sexuality. In any such populations the ratio of male-phase to female-phase individuals will depend entirely upon the proportion of young as compared with older individuals. In some other species each individual experiences several alternations of male and female phases.

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EXPERIMENTAL

It seems safe to assert that not one of the many methods which have yet been proposed for obtaining the desired sex in prospective human offspring has been proved to have any merit whatever. Nevertheless the sex ratio can be changed slightly by conditions which tend to increase or decrease the prenatal mortality. It is also theoretically possible to increase the chances of male or female offspring by choosing a mate from a family stock, if such there be, with the desired hereditary characteristics. (See *Livestock.*) In man, and in many animals and plants, maleness or femaleness is so definitely determined in the fertilized egg that no known external influence can completely reverse it. In others, on the contrary, the male-determining and female-determining factors are so nearly balanced that the sex can be controlled by relatively slight changes in the environmental conditions. In a few species of animals and plants such environmental, or phenotypic, sex control operates regularly in nature.

The environmental conditions, which in certain organisms may influence the sexuality of the individual, and hence the sex ratio of the population, may be grouped in eight categories, namely: mutilation (removal of portion of body), nutrition, chemical alteration, temperature, sunlight, delayed fertilization, association and hybridization. Not infrequently any one, of several of these may have the same effect or several may operate conjointly but it is not to be assumed that any of them, except as specially noted, are applicable to man.

The annelid worm *Ophryotrocha puerilis,* found along the seacoasts of both Europe and North America, may be mentioned as an example of this sexual instability. All the young of this species normally function as males but, on reaching a certain age and size, change to the female phase. Under favourable conditions the female phase may continue through life; but when the worm in the female phase has her posterior segments removed, or lacks sufficient food or oxygen, or is subjected to abnormal temperatures or to slightly poisonous substances, she returns to the juvenile male phase. If favourable conditions are then restored, the female phase is again resumed, but is retained only as long as such conditions continue. There are other cases in which the removal of a part of the body reverses the sexuality, both in animals and plants. Extirpation of the left gonad of the young female chicken may cause the prospective hen to develop into a cock by stimulating the otherwise rudimentary right gonad to form a testis.

Nutrition.—Both the quantity and quality of the food, as well as chemical and temperature changes, influence the sexuality of rotifers and cladoceran crustacea. Unfavourable conditions lead to the production of males from cultures of parthenogenetic females, as is also true of aphids. There is some evidence that deficient or faulty nutrition in pregnant women may be a contributing cause of abortion and thus lead to a slight decrease in the normal ratio of male births, since, as has been mentioned, the proportion of prenatal deaths, including stillbirths, is greater for males than for females.

Chemical Alterations.—Male production in cladocerans and rotifers may be elicited from their own excretions. Chemical changes in the sea water, such as the addition of a small amount of a copper or potassium salt or a trace of acid, as well as a decrease in the normal amount of magnesium, may determine whether certain worms (*e.g., Bonellia*) shall develop into males or females. Sex hormones administered to certain fishes and amphibia may likewise reverse the prospective sexuality more or less completely. In some of the amphibia such partial sex reversal may be effected by the surgical union, or parabiosis, of pairs of larvae with opposite sexuality so intimately that sex-differentiating substances may pass from one individual to the other. Grafts of heterosexual gonads may be equally effective.

Temperature may be a potent factor in sex differentiation in both animals and plants. Highly aberrant sex ratios result from temperature changes applied to the eggs of moths and other animals. If certain races of frogs are reared at a relatively high temperature, all or nearly all of the genetic females may transform into males (E. Witschi, 1942). The high temperature activates the male portion of the primary ambisexual gonad and inhibits the female portion.

Sunlight may influence the sexuality of certain plants, since improved nutrition has a tendency to initiate female development in hermaphroditic individuals.

Delayed fertilization may be influential in changing the prospective sexuality of certain amphibians and fishes. When fertilization is delayed until the eggs have become overripe, the majority or all of the resulting embryos usually develop into males.

Association in overcrowded conditions leads to male production in cladocerans. A period of attachment to the proboscis of an adult female usually causes the young, sexually undifferentiated, *Bonellia* worms to develop into males by inhibiting female development in individuals with genetic tendencies toward consecutive sexuality. In snails of the genus *Crepidula* opportunity for mating causes the accentuation and retention of the male phase in an individual which would otherwise have transformed to the female phase.

Hybridization of diverse races or species frequently results in highly aberrant sex ratios, owing in some cases to the abnormal development and death of the heterozygous sex and in other cases to the partial or complete reversal of the initial sex during development. Aberrations which may take place during the formation of the gametes may lead to the production of only one, or predominantly one, of the normally two sexual types of gametes by the heterozygous sex.

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(W. R. Ce.)

Contribution No. 375

HARALD ULRIK SVERDRUP—AN APPRECIATION

As a young man Harald Sverdrup spent seven years on Amundsen's MAUD expedition in the icy wastes of the Arctic Sea. The observations he collected during this period form the basis of fifty published papers and constitute much of our factual knowledge about geophysical phenomena in the Arctic. Nevertheless, those years of voluntary exile would be of relatively small interest to his colleagues were it not for their effect on his personal and scientific qualities, and the insight which they give into his character.

The most significant of the MAUD papers, *Dynamics of Tides on the North Siberian Shelf*, was completed for publication during the last winter in the Arctic, without adequate literature and without the benefit of discussion with colleagues. Such an accomplishment was possible only because Sverdrup had developed, to a remarkable degree, internal harmony and simplicity during the long years on the ice. These gave him an objective confidence in his own thinking and the ability to bring his thoughts to well rounded, definite conclusions. Internal harmony between the diverse aspects of a complex personality, between the explorer and the scholar, the naturalist and the theorist, the teacher and the administrator, is still Sverdrup's outstanding characteristic.

Yet the achievement during the expedition of which Sverdrup is most proud is not scientific: after seven years on the MAUD he parted friends with his shipmates. Such a feat must have required all the humor, kindliness, insight and self-discipline which characterize him today. Behind that self-discipline one occasionally glimpses a Norse emotionality, intensity and recklessness.

Sverdrup is impatient with the making of observations unless they are directed toward a definite problem. In all his papers he attempts to wring the last bit of understanding out of each number in a set of data. This frugality must derive partly from the extreme difficulty of taking field observations in the Arctic; partly it reflects his upbringing as a minister's son. Sverdrup's maternal grandfather was a professor of theology, while his paternal grandfather, a minister of the church, had five sons, all of whom became ministers, and three daughters, who married ministers.

Sverdrup was born on November 15, 1888, in Sogndal, Norway, of a family which had long been prominent in the political, religious and scientific life of the country. His cousin Otto Sverdrup was a well known explorer and captain of Nansen's ship Fram. After a boyhood spent in various parts of western Norway, Harald Sverdrup graduated with honors from the Gymnasium, then spent one year at the Academy of War where he finished as top man in athletics. In 1908 he enrolled at the University of Oslo with the intention of majoring in a subject called "Physical Oceanography and Astronomy,"—with emphasis on the latter. Three years later he was offered a job as assistant to Professor V. Bjerknes, who, with the support of an annual grant from the Carnegie Institution of Washington, was working on the application of hydrodynamics to problems in meteorology and oceanography.

During the next six years Sverdrup published twenty papers, some dealing with dynamic meteorology, others with rather formalistic properties of scalar and vector fields, and one with the radioactivity of sea water in a Norwegian fjord. The outstanding paper of this period is his doctoral dissertation, *Der Nordatlantische Passat,* which gave the first consistent picture of the dynamic and thermodynamic structure of the North Atlantic trade winds. Most of the work on his dissertation was performed while Sverdrup was distractingly hungry. He had accompanied Professor Bjerknes to Leipzig during the war and food was scarce.

At this time Sverdrup agreed to take charge of the scientific work on Roald Amundsen's North Polar Expedition on the Maud, with additional duties as navigator and part-time cook. He was 29 years old, had spent the last six years on theoretical work, discussing observations taken by others, and was anxious for a change. The expedition left Norway in July 1918, planning to come home in three or four years. Sverdrup did not return to Norway until December 1925.

Upon his return he succeeded V. Bjerknes in the Chair of Meteorology at the Geophysical Institute in Bergen, Norway. In 1931 he became research professor at the Christian Michelsen Institute. Both appointments were made with the understanding that Sverdrup could devote himself to the analysis of his Maud observations, an activity which occupied the greater part of his time up to 1933.

Among Sverdrup's published papers dealing with the cruise of the Maud are a general account of the expedition, a popular book on his personal experiences during eight months spent as a lone white man with the nomadic Chukchi tribe of northeastern Siberia, special papers dealing with meteorological observations, tides, currents, physical properties of sea water, sea ice, marine geology, aurora polaris, gravity magnetism, atmospheric electricity, astronomic observations, and *Das Tier- und Vogelleben im Treibeis.* These reports represent a general advance in many fields rather than a far reaching penetration along a narrow scientific salient. The geophysical studies reveal consummate skill in the handling of numerical data, together with a rare degree of ability to recognize physical principles underlying the data and to demonstrate these principles quantitatively by an inelegant and simple yet powerful mathematics. The strength of Sverdrup's later work lies in just this approach: the interpretation and synthesis of numerical measurements. His work is not typically characterized by interpretation of qualitative observations, nor by the development of fundamental theory.

While Sverdrup was engaged in the analysis of the MAUD data, he spent two half-year periods at the Department of Terrestrial Magnetism of the Carnegie Institution of Washington and participated in the analysis of oceanographic data collected on the seventh cruise of the CARNEGIE. In 1928 he married Gudrun Bronn Vaumund. In 1931 he was in charge of the scientific work on the Wilkins Ellsworth North Polar Expedition aboard the submarine NAUTILUS.

Sverdrup spent two months in 1934 with the glaciologist H. W. Ahlmann in the high-lying snow fields of Spitzbergen. This work in glaciology, though brief, resulted in the first quantitative study of the heat budget of glaciers and in several other important investigations. In 1936 he accepted, for a limited period, the Directorship of the Scripps Institution of Oceanography of the University of California, and accordingly took leave of absence from the Michelsen Institute for three years. He did not permanently return to Norway until March 1948.

The twelve years Sverdrup spent in California confronted him with many new problems. He had administrative responsibilities, which he discharged with thoughtfulness and distinction; he gained opportunities to teach, an activity which he enjoys and does exceedingly well. When he first came to California he had one or two students at a time; by the end of the war the need for more trained physical oceanographers had become evident, and Sverdrup organized the first systematic course in oceanography. More than two dozen students who have taken these courses will make his influence felt long after he has left the United States.

Sverdrup's effectiveness as a teacher is due only in part to the clarity and simplicity of his presentation; in larger measure it results from his modesty and his interest in human beings. He makes colleagues of his students rather than subordinates. His cultural interests outside of his work reflect the same humanism—he is concerned primarily with those works of man which give insight into the human heart.

Much of Sverdrup's research in La Jolla was directed toward problems dealing with the air-sea boundary, turbulence in the atmosphere and ocean, and upwelling. He also studied the oceanography of the Pacific, particularly the regions off southern California, and organized an expedition into the Gulf of California. His adaptability to new influences led him to become interested in the inter-relationship between marine biology and physical oceanography, and he collaborated on several papers dealing with marine biology. As an outgrowth of this widened range of interests he became senior author of a comprehensive 1100-page volume, *The Oceans, their Physics, Chemistry, and General Biology;* some of the chapters written by him were rewritten and published in a smaller companion volume, *Oceanography for Meteorologists.* In many ways Chapter XV of *The Oceans,* entitled "The Water Masses and Currents of the Oceans," is his outstanding achievement. In this 157-page chapter Sverdrup's "feeling" for data, his common sense interpretation of physical laws, his experience and remarkable memory are brought to bear upon the problem of dealing with all oceans from a common point of view. In this, as in all his work, he shows a canny judgment in selecting a productive approach to the data and in rejecting the vastly greater number of approaches which at first may seem equally promising but which lead only to inconclusive frustration.

At the outbreak of the war Sverdrup was engaged at the University of California Division of War Research on work dealing with underwater sound. Soon he had to devote his entire energy to the expanding military activities at the Scripps Institution. Among the research problems in which he personally played a leading role were the construction of current charts for life rafts, and the development of methods for predicting sea and swell for amphibious operations.

During his earlier years at Scripps, Sverdrup had been elected a member of the National Academy of Sciences and had received the Agassiz medal. At the end of the war new honors were bestowed upon him. He was elected President of the International Association of Oceanography, Vice-President of the American Geophysical Union, President of the International Commission on Polar Meteorology, and he received the LL.D. degree from the University of California. At the height of his success in America he was invited by the Norwegian Government to assume the Directorship of the new Norwegian Polar Institute. He found it very difficult to make a decision. His acceptance was based, in his own words, on his desire "to assist that small nation . . . during a period when it is struggling to get back on its feet after five years of oppression."

Thirty years ago, as a young man, Harald Sverdrup embarked for the Arctic. Now, at the age of sixty, still young in heart and mind, he is returning to those forbidding Polar regions which have given so many of their secrets to him and have played such a large part in molding his character and his scientific career. The contributors to this volume are but a few of his friends in America who wish him continuing happiness and achievement.

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Contribution No. 376

NUTRITION, ENVIRONMENTAL CONDITIONS, AND GROWTH OF MARINE BIVALVE MOLLUSKS[1]

By

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Recent investigations on the nutrition of the ciliary-feeding bivalves indicate that, although many varieties of organic and inorganic substances are ingested, most of the actual food is assimilated by the intracellular digestion of very small cells and particles. This is accomplished mainly by the phagocytic cells of the digestive organ (digestive diverticula, or "liver"), but it is aided to a small extent by migratory phagocytic cells in the lumen of the alimentary canal. The greater proportion of the ingested material consists of particles too large for this form of digestion, and the alimentary canal is deficient in most of those enzymatic extracellular secretions which are responsible for the primary digestive processes in many of the other invertebrates.

The principal extracellular secretions in the alimentary canal of these mollusks are amylase and glycogenase, secreted by the cells of the style-sac and incorporated in the style. These enzymes are set free in the stomach as the end of the style is dissolved, and they are then available for the digestion of the free starch and glycogen which may be contained in the food.

The gastric juice also contains a small amount of cellulase of the same origin, but this is evidently inadequate for the complete digestion of dinoflagellates and other phytoplankton with cellulose walls, which frequently constitute the greater part of the stomach contents. The nutritive substances contained in these organisms become available as nutrition for the bivalves only after death and disintegration into particulate materials of minute size. Only to a small extent does this occur during the short time that the ingested cells remain in the alimentary canal. Most of the living dinoflagellates pass through the canal without apparent change.

Because the stomach usually contains such a large proportion of dinoflagellates and relatively large diatoms, it was formerly assumed

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that these constituents of the phytoplankton contribute, as living cells, the greater part of the food material. However, Yonge (1926, 1935, 1946) has proved that only the smallest diatoms and similarly small organisms and particles can be assimilated by the oyster (*Ostrea lurida*). He found that the protease which would be required for the digestion of naked protoplasm or proteins could be detected in the lumen of the canal only in very small amount. Nor is there any considerable quantity of free lipase for the digestion of lipoids. The traces of these enzymes in the juices of the canal were ascribed to burst or cytolyzed phagocytes.

In his studies on the razor clam (*Ensis siliqua*), Graham (1931) likewise concluded that digestion in that species is mainly intracellular. However, he found small amounts of both amylytic and lipolytic enzymes in the midgut, with traces of the same enzymes in the rectum. He agreed with Yonge that they were due to the phagocytes present and that they were not to be considered as extracellular secretions. The style provides a strong extracellular amylase and an oxidase but no protease, lipase or invertase. Within the cells of the digestive organ (digestive diverticula) he demonstrated protease, lipase, diastase and glycogenase.

Yonge's conclusions have been supported also by the studies of Fox and Marks (1936), Fox and Coe (1943), and Coe and Fox (1942, 1944) on the sea-mussel (*Mytilus californianus*), as well as by those of Coe (1945) on the bay-mussel (*Mytilus edulis diegensis*) and Coe (1947) on the Pismo clam (*Tivela stultorum*). In all of these species, and in others less fully investigated, the gastric juice contains much amylase and glycogenase but only a small amount of cellulase. The rest of the nutrition is dependent upon the intracellular digestion of minute cells and particles within the cells of the digestive organ, supplemented by migratory phagocytes in the lumen of the alimentary canal. These cells contain within themselves the enzymes necessary for the digestion of carbohydrates, fats and proteins.

In addition to the indigestible remains of the phagocytized materials, the cells of the digestive organ excrete into the alimentary canal many of their characteristic brown granules. These are believed to be excretions and the remains of chlorophyll digestion, since all or most of them are discharged in the feces. It seems quite possible, however, that some of the digestive enzymes contained in the phagocytic cells may be secreted into the canal simultaneously, as Mansour and others maintain.

In the most primitive pelecypods (Protobranchia), digestion is reported by Yonge (1939) as being exclusively intracellular and within the cells of the digestive organ. No amylase is secreted into the stomach and there are no phagocytic cells in the lumen of the alimentary canal.

The investigations of Mansour (1946, 1946a, 1946b) and of Mansour-Bek (1946, 1946a) have led them to decide that the conclusions of the above mentioned writers are not applicable to all species of pelecypods. They report that the filtered, phagocyte-free stomach juices of *Tridacna* and *Pinctada*, and presumably of other genera, do contain proteolytic, lipolytic and carbohydrate-splitting enzymes, whereby even relatively large multicellular zooplankton can be digested. The conclusion was reached that these enzymes are set free in the canal by the fragmentation and cytolysis of ends of the phagocytic cells of the digestive organ, which are well known to contain all the enzymes mentioned. This is confirmed for *Unio* by Mansour and Zaki (1946).

A similar sloughing off of the distal portions of the phagocytic cells of the digestive organ has been reported in gastropods. Carriker (1946) and Carriker and Bilstad (1946), for example, found that in the snail *Lymnaea* the entire distal ends of some of the digestive cells are cast off in the final phase of secretion and pass into the lumens of the follicles "as an apocrine type of secretion." Nevertheless, no evidence of a protease could be detected in the gut fluids. The cells of the digestive organ here, as in the pelecypods, "function in secretion, assimilation, intracellular digestion and excretion," but in *Lymnaea* "assimilation also occurs in the pylorus and absorption possibly in the intestine." It is evident that extracellular digestion in the lumen of the canal is of minor importance.

Other gastropods, as *Crepidula* and *Vermetus*, resemble the pelecypods in their method of feeding by ciliary action and the secretion of mucus. They also resemble the pelecypods in having the alimentary canal provided with a crystalline style which supplies enzymes for the extracellular digestion of carbohydrates. The other nutrients, in the form of small particles only, are presumably digested intracellularly within the cells of the digestive organ as in the pelecypods (Yonge, 1932).

NUTRITION AND GROWTH

The rates of growth of the sea-mussel, as correlated with temperature and with the abundance of dinoflagellates, diatoms and bacteria in the water, were studied experimentally by Coe and Fox (1942, 1944) and by Fox and Coe (1943). In these experiments an average of about 100 individuals of carefully measured sizes were placed in separate compartments of wire-screened boxes and suspended below the low-water level in the vicinity of the natural mussel populations on the pier at the Scripps Institution of Oceanography. The mussels were measured at monthly intervals. In order that the boxes should always contain individuals of the same average size and age, the oldest group was discarded and replaced by young individuals after the former reached a length of about 80 mm., when growth in length decreases. The stomach contents were examined at frequent intervals. These experiments were continued for four years (1940 through 1943).

Similar studies were made by Coe (1945) on the bay-mussel, which also formed large colonies on the pier.

The nutrition and rates of growth of the Pismo clam were investigated by Coe (1947) by measuring at monthly intervals for two years (1945–1947) marked individuals living in the sand among the natural clam beds on the beach near the Scripps Institution. Large samples of the natural population were also measured at the same intervals and returned to the same positions on the beach after the measurements had been taken. Since these clams remained in their normal environment, the observed growth rates were presumably representative of the population for the two years of the experiment at the locality where the observations were made.

TABLE I. AVERAGE INCREASE IN LENGTH OF THREE SPECIES OF BIVALVE MOLLUSKS AS COMPARED WITH TEMPERATURE AND INCIDENT SOLAR RADIATION AND WITH ABUNDANCE OF DINOFLAGELLATES AND DIATOMS IN THE SAME LOCALITY DURING EACH MONTH. EACH OF THESE AVERAGES COVERS TWO YEARS. SOLAR RADIATION EXPRESSED IN TERMS OF g. cal. cm²/day.

	Av. Temp. (°C.)	*Solar radiation*	*Phytoplankton (Cells per liter)*		*Pismo clam Av. age 18 months* (mm.)	*Sea-mussel Av. age 6 months* (mm.)	*Bay-mussel Av. age 6 months* (mm.)
			Dinoflagellates	*Diatoms*			
Oct.	18.4	331	23,000	18,000	2.1	5.0	6.4
Nov.	15.6	303	10,000	4,000	1.7	4.3	5.9
Dec.	14.4	214	5,000	2,000	1.2	3.5	5.1
Jan.	13.2	246	2,000	1,000	0.9	3.2	3.8
Feb.	13.3	309	3,000	27,000	0.7	3.1	3.2
Mar.	14.2	461	12,000	20,000	1.2	4.1	4.2
Apr.	16.0	440	23,000	22,000	2.0	5.2	5.3
May	17.8	566	53,000	50,000	2.3	5.8	6.3
June	19.4	524	108,000	42,000	2.4	5.6	6.7
July	19.8	561	98,000	50,000	2.3	5.5	6.5
Aug.	20.6	508	20,000	107,000	2.0	5.3	6.3
Sept.	19.2	430	28,000	42,000	2.3	5.5	6.6
Average increase per year					21.1	56.1	66.3

RATES OF GROWTH

As indicated in Table I and Fig. 1, both the bay-mussel and the clam showed a maximum rate of growth in June and a minimum in January and February, the months of average lowest temperature. For the sea-mussel the maximum was in May and the minimum from December to February. All of the three species showed a slight decrease in

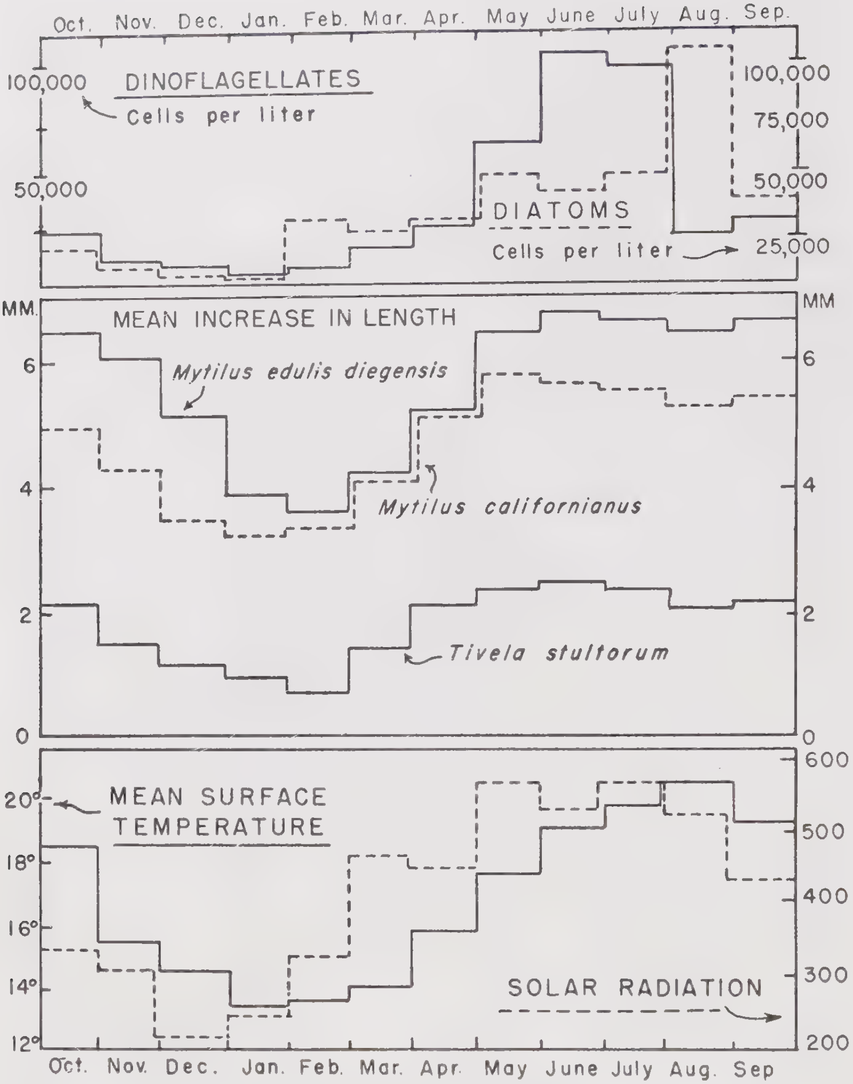

Figure 1. Correlation between temperature, solar radiation, abundance of dinoflagellates and diatoms and mean monthly increase in length of three species of bivalve mollusks under natural conditions at the Scripps Institution of Oceanography. The measurements indicated for each species represent the averages for two years. The data for the clam are based on measurements made in 1945–47, while the other data are taken from the records of the preceding years. The growth rates are more nearly parallel with the abundance of dinoflagellates than with the other environmental conditions. The incident solar radiation is shown in terms of g. cal. cm² per day.

August, the month of highest temperature, followed by a rise in September.

Fox and Coe (1943) found that the average length of the sea-mussels in the experimental boxes at the age of one year was 56.1 mm., the maximum length observed at that age being 86 mm. There was a gain in length of about 45 mm. during the second year and 25 mm. during the third year. The dry weights of the body tissues at one, two and three years of age averaged 2, 5.6, and 8 g. respectively, and of the shell at the same ages 23.5, 70, and 104.59 g., respectively. It will be observed that while the increase in length during the second year was little more than half the increment of the first year, the volume, weight of tissues, and weight of shell was more than doubled.

The bay-mussel grew more rapidly than the sea-mussel under the same conditions during its first year but more slowly during its second year. A mean length of about 66.3 mm., with an observed maximum of 82 mm., was attained at the age of one year, and a maximum of about 93 mm. at the age of two years. Thereafter the rate of growth was very slow; few individuals in the local population exceed 105 mm.

The Pismo clam grows much more slowly than either species of mussel, the maximum observed length at one year of age being only 31 mm. and the average 21.1 mm. This rate shows but little diminution during the next two years, but decreases thereafter. In the local population a maximum length of 150 mm. with a shell weight of 600 g. at the age of ten to twelve years has been observed, but larger individuals have been reported from other parts of the coast. The growth rates of this species, as indicated by large collections of the population for each month of the two years 1945–47, as well as by marked individuals, are shown in Fig. 2. On some beaches on the California Coast, particularly those contaminated with sewage, the growth rates are greater and in other localities less than here recorded for La Jolla.

Sources of Nutrition

At all seasons of the year the greater part of the stomach contents of all the ciliary-feeding bivalves investigated consists of detritus and phytoplankton, particularly dinoflagellates and diatoms, together with much inert material, such as particles of sand, tiny fragments of mollusk shells and small pieces of algae. Included also, but in much smaller amount, are the more minute particles and organisms mentioned below as forming the principal part of the nutrition. There is little or no selection from among these particles except for size, although spiny objects are generally excluded.

The water about the mussel and clam beds at the Scripps Institution of Oceanography is reported to contain an average of about .005 g. of

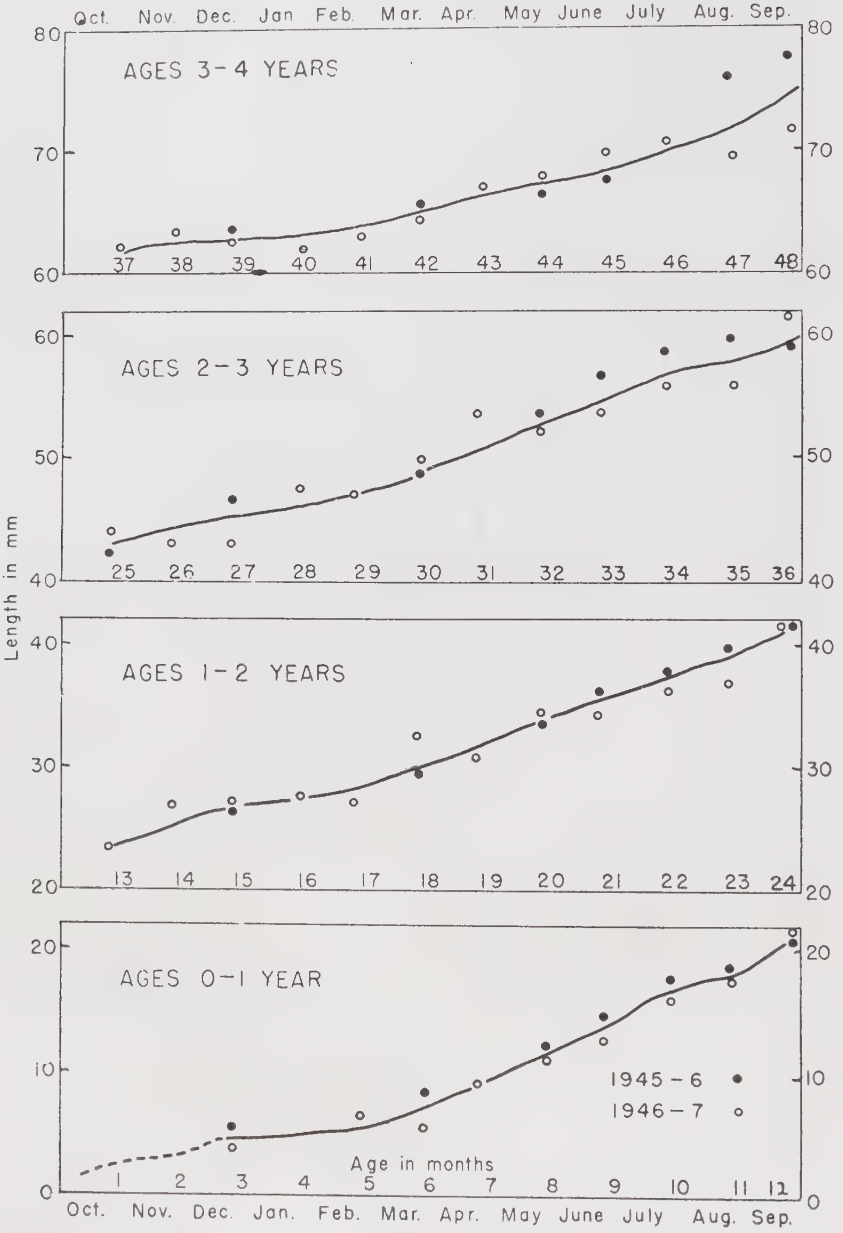

Figure 2. Increase in length of Pismo clam as determined by large samples of the population on the beach at the Scripps Institution of Oceanography taken at monthly intervals during two years. All the clams were returned to the same part of the beach after the measurements had been made. The lower rates of growth in winter and in the month of August are indicated.

total dry organic matter per liter. Some of this is in solution and consequently is unavailable to the mollusks until after it has been converted into particulate or colloidal materials by the action of bacteria or other unicellular organisms. If all were available and if the average adult bivalve filters 22,000 liters of water per year, as estimated by Fox and Coe (1943), there would be a potential supply of 110 g. for each bivalve. Of this the animal stores 1 to 2 g. in the body and discharges as gametes 1 to 3 g. annually (Table II).

TABLE II. Materials Ingested by Ciliary-Feeding Bivalve Mollusks

	Ingested	*Digested*	
		Living	*Dead (as detritus)*
a. Phytoplankton			
1. Dinoflagellates; 32,000 per l., 12 g.*	+	−	+
2. Diatoms; 32,000 per l., 1.5 g.*	±	±	+
3. Bacteria; 45,000,000 per l., 0.05 g.*	+	+	+
4. Other unicellular and multicellular algae	±	−	+
5. Zoospores and other reproductive cells	+	±	+
b. Zooplankton and nekton			
1. Flagellates	+	±	+
2. Rhizopods and ciliates (including tintinnids)	±	±	+
3. Reproductive products of invertebrates			
Ova and larvae	±	−	+
Spermatozoa	+	+	+
4. Invertebrates and vertebrates	−	−	+
c. Benthic algae and eelgrasses	−	−	+
d. Benthic invertebrates	−	−	+
e. Inorganic and refractory	±	0	0

* Quantity, where given, indicates amount of dry organic matter potentially ingested by one adult individual in one year. Based on computations by Fox and Coe (1943) for a single sea-mussel 70 mm. in length filtering 2.5 l. of water per hour or 22,000 l. per year.

The sign + indicates generally; ± commonly, but only small individuals or species; − rarely or not at all.

All the organic matter in the sea, except those refractory materials such as cellulose, lignin, chitin and others which the mollusks are unable to digest, may be considered as potential nutrients for both mussels and clams. These become available either as the constituents of minute living cells or, more abundantly, as detritus after the death of unicellular and multicellular animals and plants and the disintegration of their cells. Eventually even the refractory organic materials may become available through the action of bacteria.

Therefore, the potential food supply will obviously include: *A*, phytoplankton, consisting of dinoflagellates, diatoms, bacteria and other unicellular and multicellular algae and their reproductive cells; *B*, zooplankton and nekton, including various flagellates, foraminifera and other rhizopods, tintinnids and other ciliates, as well as all invertebrates and vertebrates, with their reproductive cells and larvae;

and for completeness, *C*, all the benthic animals and plants, since they supply no small part of the detritus (Table II). It is obvious that the detritus may be of local origin or brought from a distance by the ocean currents.

PHYTOPLANKTON

The amount of phytoplankton in the water at the Scripps Institution pier is highly variable from year to year and even from month to month. Furthermore, there may be several times as many of the constituent organisms on one day as on the next or preceding day because of the ocean currents which transport the water to and from the area at an average velocity of 4 to 5 miles a day.

In their studies on the nutrition and growth of the sea-mussel, Coe and Fox (1944) have shown that, during the four years 1940 through 1943, those months and those years with the largest dinoflagellate populations were generally conducive to the highest growth rate of the mussels, but that the same correlation did not hold for the diatoms.

Combining the four years gives an average of about 32,000 dinoflagellates per liter, with an approximately equal number of diatoms (Table I, Fig. 1). The dinoflagellates reached a maximum concentration during May, June and July, with a minimum in January and February. In those years there was a sharp decrease in August, the month with the highest temperature of the water, with an increase in September, followed by a gradual decline during the remainder of the year. The diatoms, on the other hand, reached a miximum in August, with a sharp decline toward the end of the year (Fig. 1; Table I).

Over a period of 20 years preceding 1940 there has been a general tendency for both diatoms and dinoflagellates to reach their highest productivity at about the same season of the year. For both groups the period of highest average abundance has been from April to July, with the lowest average in December and January. For several years the lowest average was in August, while in other years the highest average was in that month (Allen, 1940).

Table I, Fig. 1 show that there is some degree of correlation between the monthly averages of both dinoflagellates and diatoms (particularly of dinoflagellates) and the growth rates of mussels and clams, but it should be mentioned again that the dinoflagellates are not utilizable while living and most of the diatoms are too large for intracellular digestion. Such correlations as were found in these experiments are therefore thought to be only indirect and to indicate merely that environmental conditions favorable to the production of large dinoflagellate populations are likewise favorable to the rapid growth of ciliary-feeding mollusks. These studies offer additional evidence of the complexity and variation of the environmental conditions which influence the organisms living on the shores of the oceans.

1. *Dinoflagellates.* The amount of nutrition potentially available (mainly in the form of detritus) from the principal constituents of the phytoplankton has been computed by Fox and Coe (1943) for the sea-mussel, by Coe (1945) for bay-mussel and by Coe (1947) for the Pismo clam. It was estimated that one of these bivalves, on reaching a length of 70 mm., would filter about 60 liters of water during its feeding time each day, or 22,000 liters in a year. With an average dinoflagellate population of 32,000 cells per liter, a total of about 700 million would be available for each individual during the year. If, as estimated, 60 million cells yield 1 g. dry organic matter, then the dinoflagellates presumably ingested in a year would have supplied nearly 12 g. dry organic matter if taken as detritus.

2. *Diatoms.* Similarly, the 32,000 diatoms available per liter would supply only 1.5 g. of organic matter in a year, since these organisms are so small that 500 millions of average size would yield only 1 g. dry organic matter. Most of these, as has been stated, are capable of being digested by the mollusks only after they have become detritus.

3. *Bacteria.* The water in the vicinity of the clam and mussel beds contains an average of about 45 million bacterial cells per liter, and although they are readily ingested and assimilated, they are so minute that they yield but a fraction of a gram of dry organic matter. It is quite possible, however, that they may supply nutritive elements not otherwise available.

4. *Other Unicellular and Multicellular Algae.* Because of their usual cellulose walls, algal cells resist digestion by the bivalve mollusks, but all algae provide nutritive detritus from their cell contents after death and disintegration. Cryptomonads, phytomonads and some of the other flagellates are often abundant and small enough for intracellular digestion. They undoubtedly contribute largely to the bivalves' nutrition.

5. *Zoospores and Other Reproductive Cells of Algae.* These are often very abundant and those that are without cellulose walls are readily ingested and digested. They also become available as detritus.

Zooplankton and Nekton

Only the smallest protozoa are capable of being digested by the intracellular method characteristic of the bivalves, although somewhat larger forms are readily ingested.

1. *Flagellates.* The water often contains vast numbers of various species of flagellates of so minute a size that they are readily available in the living condition. Bruce, Knight and Parke (1940) and others have demonstrated the necessity of these organisms for the normal nutrition of oyster larvae. It seems reasonable to assume that other bivalve mollusks may have the same requirements. Only occasional records are available relative to the numbers of these minute flagellates in the water at different seasons of the year, but it is known that at times they may exceed both the dinoflagellates and diatoms in abundance, with more than a million per liter.

2. *Rhizopods and Ciliates.* With the exception of the flagellates, most of the protozoa are too large for intracellular digestion, but some of them produce reproductive cells which are readily available. Furthermore some of the tintinnids are of the requisite degree of minuteness. All become available after disintegration as detritus.

3. *Reproductive Products of Invertebrates.* Some of the echinoderms and other invertebrates in the vicinity of the clam and mussel beds, including the clams and mussels themselves, set free in the water at certain times of the year vast numbers of spermatozoa. These are admirably adapted for intracellular digestion. The ova and larvae of many species are likewise ingested readily, but since the alimentary canal is deficient in the protease which would be necessary for their digestion, their materials usually become available only after cellular fragmentation. This may occur within the digestive system of the mollusk.

4. *Invertebrates and Vertebrates.* The disintegration of the cells composing the bodies of all the invertebrates and vertebrates of the vicinity, together with their reproductive cells and larvae, provide, after death, an abundant detritus which undoubtedly supplies a large proportion of the bivalves' nutrition. Much of the detritus of local origin is carried elsewhere by the ocean currents, but this is replaced by supplies brought from a distance by the same currents.

Benthic Algae and Eelgrasses

Detritus from these sources is always available and doubtless furnishes a considerable proportion of the nutrition after the disintegration of the contents of the cells.

Benthic Invertebrates

It seems probable that the vast populations of invertebrates (including the bivalves) along the coast provide a greater quantity of nutritive detritus from their disintegrated bodies, from their gametes and from their feces and excretions than all the other organisms combined.

CHEMICAL AND PHYSICAL CONDITIONS

Chemical Conditions. In localities where there are appreciable changes in the salinity of the sea water, or where toxic substances are added or developed by decomposition or otherwise, the growth rates of the mollusks may be profoundly affected. At the Scripps Institution of Oceanography, however, the rainfall is normally so low as to have little effect on the salinity, and there are no rivers in the vicinity. As a consequence, changes in the chemical composition of the water are too small to influence the growth of the marine invertebrates except in very exceptional seasons. However, there are occasional periods when excessive populations of dinoflagellates, usually in midsummer, may seriously and adversely affect the growth and even the vitality of the mollusks.

Physical Conditions. The graphs in Fig. 1 and the data in Table I indicate considerable differences in the growth rates of both mussels and clams during different months of the year. These appear to be correlated with temperature and solar radiation, as well as with the abundance of phytoplankton. The Scripps Institution is situated on the open coast and is therefore fully exposed to the violence of the surf at the times of occasional storms, usually in the winter.

Whenever these storms occur, not only do the mollusks remain closed and stop feeding, but some of the mussels are torn from their moorings and many of the clams are dislodged by the shifting of the sand, while others are compelled to change their positions in the sand. Since the periods of the storms usually coincide with the season of low temperature, decreased solar radiation and minimum phytoplankton populations, it has seemed impossible to calculate the effects of each of these conditions separately. However, the combined effects of these factors, and presumably others, result in a decreased growth rate of the clam to about one-third and of the mussels to about one-half of the rates characteristic of the most favorable months of the year (Fig. 1, Table I).

TEMPERATURE

Both the mussels and the clams were found to grow most rapidly when the temperature of the water was from 17 to 20° C. Feeding and growth continue, but at a much lower rate, at temperatures of 14° or lower. Experimental evidence was obtained that mussels continue to feed at temperatures as low as 7 to 8° and as high as 25 to 26°, although both these extremes are far beyond the conditions found in nature at La Jolla. In other regions mussels may continue their activities at a temperature of 0° or lower.

Loosanoff (1942) found that on the coast of southern New England the bay-mussel, *Mytilus edulis*, may remain open and active at temperatures ranging from −1.0° to 24.9° C. Feeding continued at or near 0° C. There was a rather close correlation between growth rate and temperature.

Richards (1946) has compared the growth rates of *Mytilus californianus* at La Jolla, California, with those of *M. edulis* at Woods Hole, Massachusetts, with respect to the phytoplankton, temperature and solar radiation. In the latter locality the winter and summer temperatures often differ by as much as 20° C. and at La Jolla by 5° to 8° C. At Woods Hole the maximum rate of growth was in April, followed by a reduced rate in summer and a marked increase in autumn. He concluded that the growth rates in both localities are proportional to the solar radiation but are complicated by changes in food content and temperature of the water.

In more northern localities, both on the coasts of Europe and North America, the annual increment in size is greatly decreased as compared with regions farther south where the temperatures favorable for rapid growth are of longer duration.

On the coast of Norway the growth of the horse-mussel (*Modiola modiolus*) is even slower than that of any of the species mentioned above for localities where the water is considerably warmer. Wiborg (1946) found that the annual increase in length of the young mussels was usually only 6 to 10 mm. a year, with an observed maximum of 15 mm. Individuals 8 years old had an average length of 55 mm., those 10 years old measured 65 to 79 mm., and those 18 years old 98 to 118 mm. Growth was comparatively rapid from July to October but almost ceased as the temperature fell to a minimum during December to April.

SOLAR RADIATION

It is obvious that photosynthesis, and consequently the growth and multiplication of the phytoplankton, is largely dependent on the amount of solar radiation. At the Scripps Institution of Oceanography the incident solar radiation, or insolation, in terms of gram-calories cm^2 per day in the years under consideration reached a maximum in May and July and a minimum in December (Fig. 1; Table I). The abundance of phytoplankton, as well as the growth rates of the bivalve mollusks, follow somewhat similar curves but with many variations for these two years. The similarity of the curves would undoubtedly be increased over a longer term of years.

The graphs (Fig. 1) show that while the solar radiation reached a minimum in December, the lowest populations of phytoplankton occurred one month later, as did also the minimum growth of the sea-mussel. The minimum for the bay-mussel and the Pismo clam was delayed until February, due in part to the influence of storms and the accompanying heavy seas. The maximum solar radiation in May was accompanied by the maximum growth of the sea-mussel. This was followed one month later by the maximum abundance of dinoflagellates and by the most rapid growth of the other two species of bivalves. The maximum population of diatoms in August in these two years likewise followed the maximum solar radiation in July. This was exceptional however, for, as already mentioned, the maximum abundance of diatoms more often occurs in April, following a high period of solar radiation in March and the accumulation of inorganic nutrients during the winter.

SUMMARY

Recent investigations on the nutrition of ciliary-feeding bivalves confirm the evidence that free starch and glycogen are digested in the stomach by enzymes secreted by the cells of the style-sac and incorporated in the style. The gastric juice also contains a small amount of cellulase, but this is inadequate for the complete digestion of dinoflagellates and other phytoplankton with cellulose walls.

All, or nearly all, the rest of the nutrition is derived from the digestion of minute cells and particles within the cells of the digestive organ, supplemented by migratory phagocytes in the alimentary canal. A large proportion of the nutritive materials consists of detritus derived from the disintegration of the cells of unicellular and multicellular plants and animals.

A considerable degree of correlation is found between the growth rate during each month of the year and the food supply, temperature, solar radiation and other environmental conditions.

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Contribution No. 377

REFLECTION OF TSUNAMIS[1]

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INTRODUCTION

Waves are reflected whenever they move into a region where their speed of propagation changes. It has generally been found that for appreciable reflection a large change in speed of propagation must occur over a distance which is small compared to a wave length. Since tsunamis are shallow water waves, they are propagated at a speed c which depends on the depth h according to

$$c = \sqrt{gh} .$$

A typical tsunami, one having a period of 20 minutes for example, has a wave length of 90 miles in water of 5,000-ft. depth. At the continental slopes and walls of deep oceanic trenches, an appreciable depth change takes place over a distance which is small compared with this typical wave length, and reflection is to be expected. The object of this paper is to examine the observational evidence for tsunami reflection and to make a comparison with results which are derived theoretically.

OBSERVATIONAL EVIDENCE OF REFLECTION

Occasionally a tide gauge record of a tsunami shows a marked amplitude increase long after the arrival of the first waves. Such a feature has been considered as possible evidence of reflection if its time of occurrence coincides with the expected arrival time of waves traveling

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[2] We would like to take this occasion to express our great appreciation for the privilege of working and studying under the direction of Dr. H. U. Sverdrup. The training and guidance which he has provided have been and will continue to be invaluable to us.

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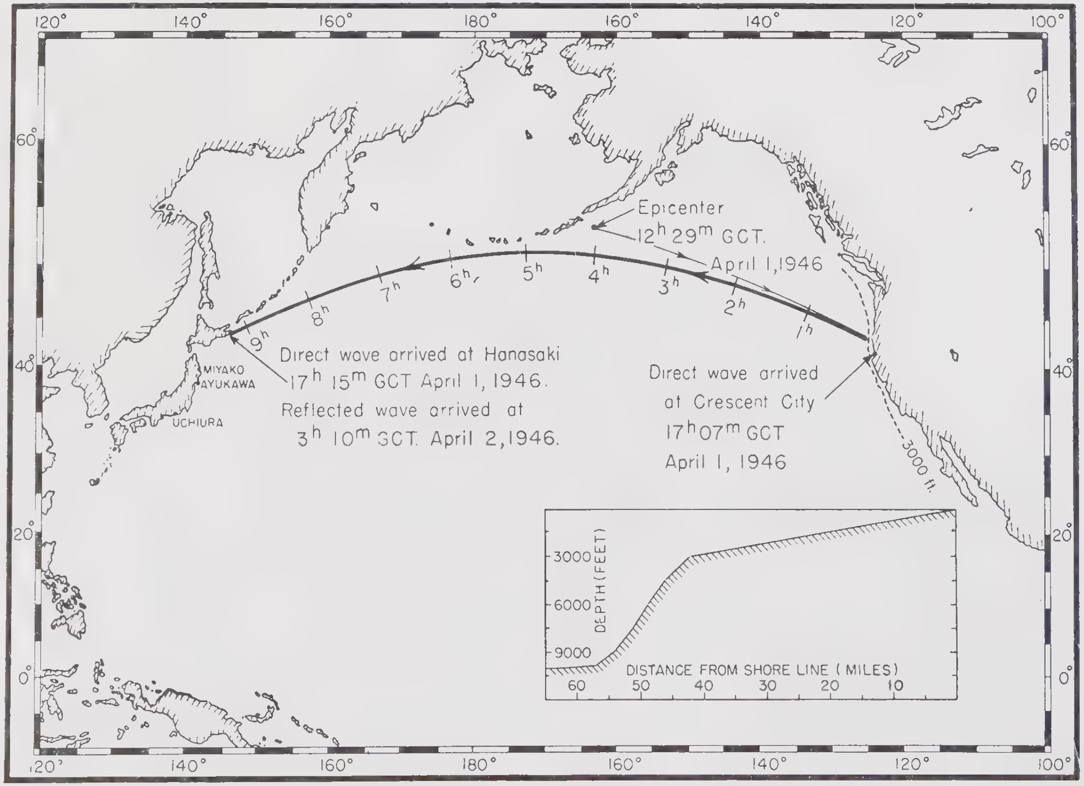
120°
140°
160°
180°
160°
140°
120°
100°
60°
40°
20°
0°
Epicenter
12^h 29^m GCT.
April 1,1946
1^h
2^h
3^h
4^h
5^h
6^h
7^h
8^h
9^h
Direct wave arrived at Hanasaki
17^h 15^m GCT April 1, 1946.
Reflected wave arrived at
3^h 10^m GCT. April 2, 1946.
Direct wave arrived
at Crescent City
17^h 07^m GCT
April 1, 1946
3000 ft.
MIYAKO
AYUKAWA
UCHIURA
DEPTH (FEET)
3000
6000
9000
DISTANCE FROM SHORE LINE (MILES)
60
50
40
30
20
10

Figure 1. Arrival times at Hanasaki of direct and reflected waves for tsunami of April 1, 1946. Heavy solid line indicates probable path of reflected waves reaching Japanese Coast. Inset shows a typical bottom profile along a line from shore near Crescent City.

over a path involving at least one reflection. Amplitude variations appear frequently in records of tsunamis. The evidence for reflection is most conclusive, therefore, when the amplitude increases greatly during a short interval of time and then remains relatively large for a period of several hours.

Two records discussed by Hart (1931: 192–198) are ideal in this respect, since the tsunamis were associated with earthquakes east of New Zealand, and the records show no indication of tsunami-type waves at Sydney until the arrival of waves supposedly reflected. Of about 25 additional records examined by the present writers, those from four Japanese stations (location in Fig. 1) for the tsunami of April 1, 1946 contain indication of reflection[3] (Figs. 2–5), and of these only the evidence from Hanasaki is conclusive.

To bring out the general trend of wave height, individual wave heights were averaged in overlapping two-hour intervals centered at each of the first 20 hours of the tsunami. The arrival of a train of reflected waves may be expected to show up as a relatively steep slope in the curve of average height.

The first few waves were small in all four cases, hardly exceeding 10 cm. at most. After seven to ten hours had passed, the average heights had increased two- to seven-fold (Figs. 2–5). The most sudden increase occurred at Hanasaki, where the average height grew from 6 cm. to 24 cm. in the time interval 0200 to 0500 G. C. T. The slope of the curve of average height is steepest at 0310 G. C. T., 9 hr. and 55 min. after the arrival of the first wave. A rough refraction diagram indicates that waves could reach Hanasaki by way of a reflection at or near the coast of southern Oregon (Fig. 1). The expected time interval from the arrival of the first wave to the arrival of such a reflected wave is 9 hr. and 24 min., which is close to the interval actually observed.

THEORY

The reflecting mechanisms which are considered in this paper are the rather abrupt changes in depth embodied in the continental slopes and walls of deep oceanic trenches. As a first approximation, the size of reflected waves is calculated for a simple model defined as follows:

1) The depth changes abruptly along a straight line (Fig. 6, showing the co-ordinate system which is used).

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[3] Evidence from records and a refraction diagram received from the Japanese Central Meteorological Observatory through the Hydrographic Office, Department of the Navy. In the refraction diagram prepared by the observatory, wave trains reflected near various sections of the North American coast are shown.

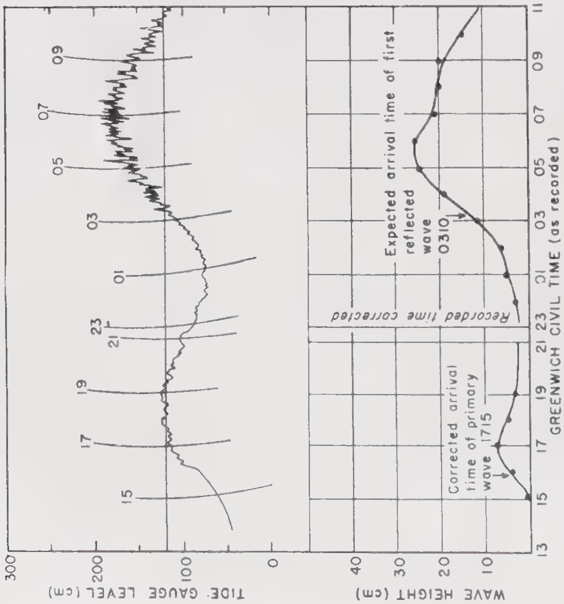

FIGURE 2. Hanasaki tide gauge record for tsunami of April 1, 1946, and graph of average wave height.

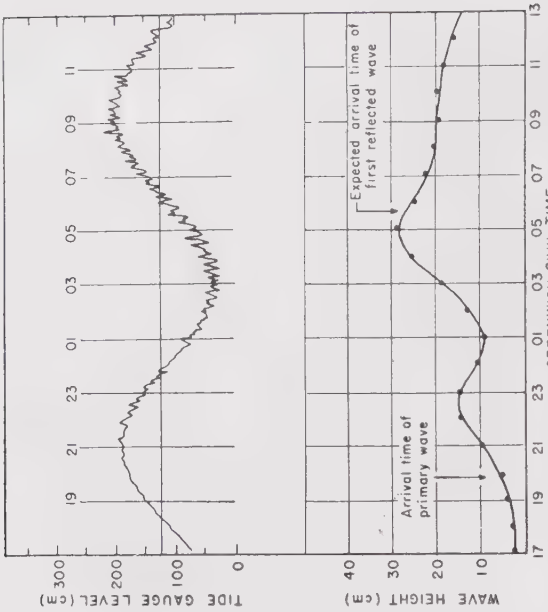

FIGURE 3. Miyako tide gauge record for tsunami of April 1, 1946, and graph of average wave height.

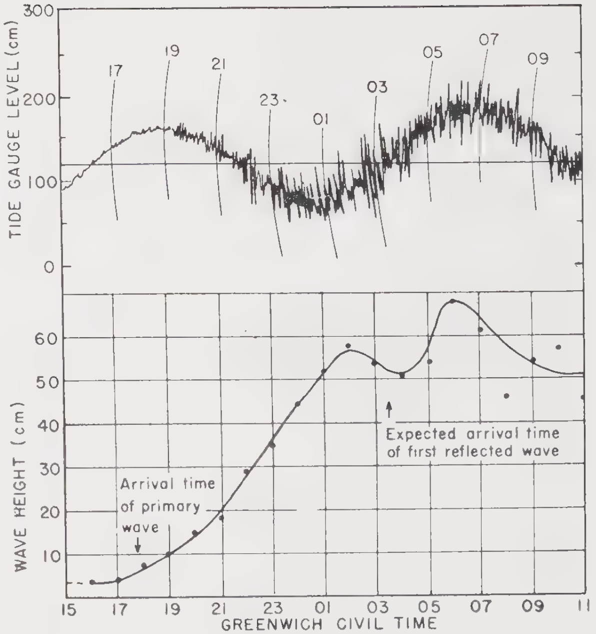

FIGURE 4. Ayukawa tide gauge record for tsunami of April 1, 1946, and graph of average wave height.

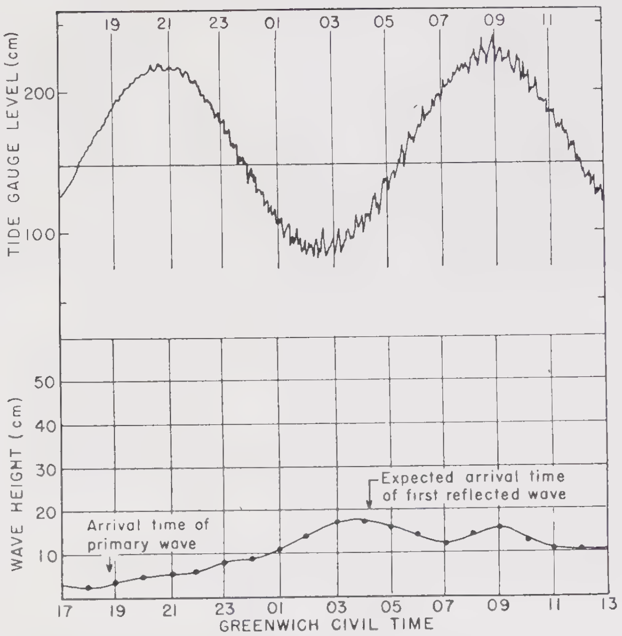

FIGURE 5. Uchiura tide gauge record for tsunami of April 1, 1946, and graph of average wave height.

2) The waves striking this discontinuity in depth are plane and sinusoidal.
3) The ratio of the depth h to the wave length L is less than 0.05, so that the theory of "shallow water" waves holds.
4) The amplitude of the displacement of the free surface, ζ, is very small compared with L and h.

The differential equation of waves satisfying conditions (3) and (4) of the model is for $x > 0$ (Fig. 7)

$$\frac{\partial^2 \zeta_1}{\partial t^2} = c_1^2 \left(\frac{\partial^2 \zeta_1}{\partial x^2} + \frac{\partial^2 \zeta_1}{\partial y^2} \right), \quad (c_1 = \sqrt{gh_1}) ,$$

and for $x < 0$,

$$\frac{\partial^2 \zeta_2}{\partial t^2} = c_2^2 \left(\frac{\partial^2 \zeta_2}{\partial x^2} + \frac{\partial^2 \zeta_2}{\partial y^2} \right), \quad (c_2 = \sqrt{gh_2}) .$$

Solutions providing for plane sinusoidal incident and reflected waves on the negative-x side, and transmitted waves on the positive-x side, are:

$$\zeta_1 = A_1 \cos \sigma \left(t + \frac{\mu_1 x + \nu_1 y}{c_1} \right) + A_1' \cos \sigma \left(t + \frac{\mu_1' x + \nu_1' y}{c_1} \right), \tag{1}$$

$$\zeta_2 = A_2 \cos \sigma \left(t + \frac{\mu_2 x + \nu_2 y}{c_2} \right), \tag{2}$$

where $\sigma = 2\pi/T$, T being the period,

and
$$\begin{aligned} \mu_1 &= \cos \theta_1, & \nu_1 &= \sin \theta_1, \\ \mu_1' &= \cos (\pi - \theta_1') = -\cos \theta_1', & \nu_1' &= \sin (\pi - \theta_1') = \sin \theta_1', \\ \mu_2 &= \cos \theta_2, & \nu_2 &= \sin \theta_2; \end{aligned}$$

these angles being shown in Fig. 7.

The displacement, ζ, and mass transport perpendicular to the discontinuity in depth, $\rho h u$, are continuous across the discontinuity. That is, at $x = 0$

$$\zeta_1 = \zeta_2, \tag{3}$$

and

$$\rho h_1 u_1 = \rho h_2 u_2. \tag{4}$$

Since u is proportional to $\partial \zeta / \partial x$ for sinusoidal waves, (4) may be expressed by

$$h_1 \frac{\partial \zeta_1}{\partial x} = h_2 \frac{\partial \zeta_2}{\partial x} . \tag{4'}$$

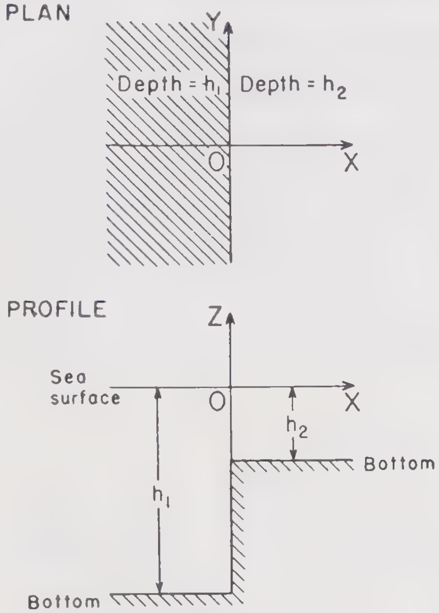
PLAN
Y
Depth = h_1
Depth = h_2
O
X
PROFILE
Z
Sea surface
O
X
h_2
Bottom
h_1
Bottom

FIGURE 6. Schematic diagram showing abrupt depth change assumed in theory.

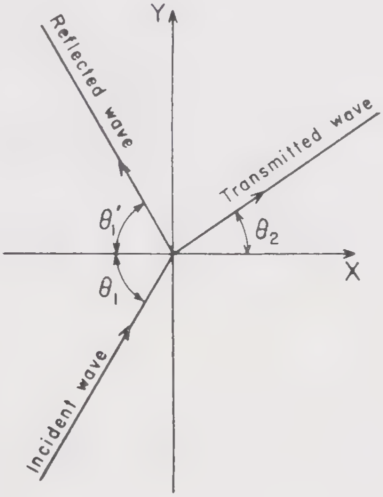
Y
Reflected wave
Transmitted wave
θ_1'
θ_2
X
θ_1
Incident wave

FIGURE 7. Direction of travel of incident wave, reflected wave, and transmitted wave.

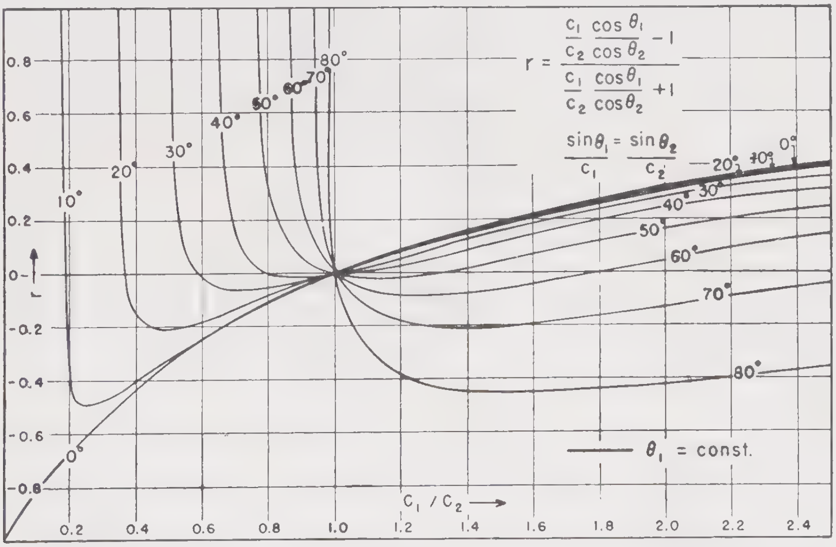

FIGURE 8. Amplitude coefficient of reflection, r, as a function of the velocity ratio, c_1/c_2, for various values of the angle of incidence θ_1.

Substituting (1) and (2) into (3) and (4′) gives

$$A_1 + A_1' = A_2, \tag{5}$$

and

$$\frac{h_1\mu_1A_1}{c_1} + \frac{h_1\mu_1'A_1'}{c_1} = \frac{h_2\mu_2A_2}{c_2}, \tag{6}$$

at $x = y = 0$. It follows from (5) and (6) that the ratios A_1'/A_1 and A_2/A_1 are given by

$$\frac{A_1'}{A_1} = \frac{c_2\mu_2 - c_1\mu_1}{c_1\mu_1' - c_2\mu_2}, \tag{7}$$

and

$$\frac{A_2}{A_1} = \frac{c_1\mu_1' - c_1\mu_1}{c_1\mu_1' - c_2\mu_2}. \tag{8}$$

The ratio A_1'/A_1 is called the amplitude coefficient of reflection and will be denoted by r. The ratio A_2/A_1 is called the amplitude coefficient of transmission and will be denoted by s.

The law of reflection,

$$\theta_1 = \theta_1',$$

implies that

$$\mu_1 = \cos\theta_1 = \cos\theta_1' = -\mu_1'.$$

Equations (7) and (8) can therefore be written

$$r = \frac{c_1\cos\theta_1 - c_2\cos\theta_2}{c_1\cos\theta_1 + c_2\cos\theta_2}, \tag{7′}$$

and

$$s = \frac{2\,c_1\cos\theta_1}{c_1\cos\theta_1 + c_2\cos\theta_2}. \tag{8′}$$

The case of normal incidence has been treated by Lamb (1932: 262).

Snell's law,

$$\frac{\sin\theta_1}{c_1} = \frac{\sin\theta_2}{c_2},$$

makes it possible to obtain r as a function of c_1/c_2 for any given values of the angle of incidence θ_1. This relation is shown graphically in Fig. 8.

An important feature of the relation which can be seen from the graph is that r changes very little between an angle of incidence of 0° and 20°, when $c_1/c_2 > 1$, that is, when the incident waves approach a decrease in depth. Another noteworthy feature of the relation is that there is a critical angle of incidence when $c_1/c_2 < 1$, that is, when the incident wave approaches an increase in depth. If the angle of incidence exceeds this critical value, total reflection is indicated ($r = 1$).

The reflection coefficient has been derived on the assumption of an abrupt depth change. The theory of reflection of sound from a region between two parallel planes where the speed of propagation increases (or decreases) gradually indicates that the reflection coefficient depends on the ratio

$$\frac{d}{L/\sin\theta},$$

where d is the perpendicular distance between the planes, L the wave length, and θ the angle of incidence. If the ratio is small, the reflection coefficient is nearly as large numerically as it is for a discontinuous change. If the ratio is large, the reflection coefficient is nearly zero. Assuming the same criterion to apply to tsunamis, the reflection coefficient calculated above (Eq. 7′) is a fairly good approximation at steep slopes. For example, at the Continental Slope off northern California (near Crescent City) the depth increases from 3,000 to 9,900 ft. in about 15 mi.[4] (Fig. 1, inset). The wave length of a tsunami with 15 min. period in a depth of 9,900 ft. is 116 mi. For normal incidence the ratio

$$\frac{d}{L/\sin\theta} = \frac{15}{116} = 0.13\,.$$

APPLICATION OF THEORY

Of various tide gauge records, that taken at Hanasaki can be used most satisfactorily to check the validity of the theoretically derived reflection coefficient. Since the direct waves were very small, the heights after the arrival of reflected waves are considered to result entirely from the reflected waves.

As noted above, the reflected waves which reached Hanasaki appear to have been reflected from the Continental Slope off southern Oregon. The height of waves reflected there can be estimated from the heights recorded at Cresent City (Fig. 9a), the nearest station from which

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[4] Miles refers to statute miles throughout this paper.

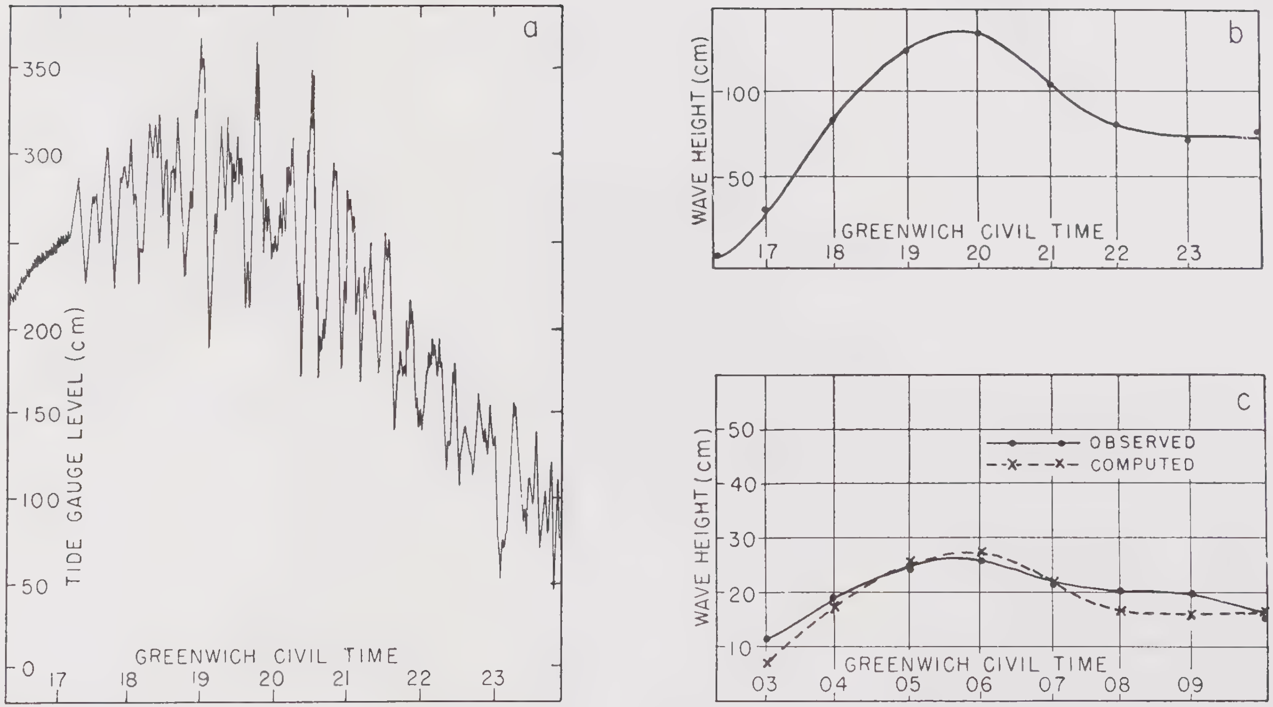

Figure 9. a. Crescent City tide gauge record for tsunami of April 1, 1946. b. Graph of average wave height for Crescent City. c. Comparison between observed and computed average wave heights at Hanasaki.

records are available. The heights averaged over two hour intervals, H_C, have been computed for each of the first 10 hours (Fig. 9b) in the same manner as they were for Hanasaki.

A typical bottom profile along a line seaward from near Crescent City is shown in the inset of Fig. 1. To facilitate computation, the bottom contours have been assumed to be straight lines parallel to the coastline. The actual contours do not differ widely from this picture.

Since the waves approach the coast almost at right angles, they diverge very little, and so Green's law (Lamb, 1932: 275),

$$\frac{H_1}{H_2} = \left(\frac{h_2}{h_1}\right)^{1/4},$$

can be used to obtain an estimate of the wave heights at 3,000 ft. from the recorded wave heights at Crescent City. The depth of the water at the tide well is assumed to be 20 ft. Thus the wave height at 3,000 ft., H_{3000}, is given by

$$H_{3000} = H_C\left(\frac{20}{3000}\right)^{1/4}. \qquad \text{(A)}$$

The height of waves reflected from the slope at 9.900 ft. is obtained by applying the theory developed above. The reflection and transmission coefficients for incidence at 10° are nearly the same as those for normal incidence, namely

$$r = 0.27,$$

$$s = 1 + r = 1.27,$$

for $c_1/c_2 = \sqrt{9900/3000}$. The height of waves reflected at 9,900 ft., H_R, is then given by

$$H_R = \frac{r}{s} H_{3000} = \frac{0.27}{1.27} H_{3000}\,. \qquad \text{(B)}$$

Reflection along the path (Fig. 1) of the reflected wave from the slope off southern Oregon to the Japanese Trench can be neglected, since there are no abrupt changes in depth.

The effect of distance D on the waves is obtained by using the relation

$$\frac{H_1}{H_2} = \left(\frac{D_2}{D_1}\right)^{1/3},$$

which applies to the first few waves of an impulsively generated wave train (Jeffreys, *et al.*, 1946: 485). In the present calculation D_1 is approximately 1,900 mi., and D_2 approximately 6,300 mi. The height off Hanasaki, at 9,900 ft., is given by

$$H_J = \left(\frac{1900}{6300}\right)^{1/3} H_R \, . \tag{C}$$

The height at the Hanasaki tide well, H_H, is obtained from H_J by Green's law. The depth of water at the tide well is again assumed to be 20 ft. Thus

$$H_H = \left(\frac{9900}{30}\right)^{1/4} H_J \, . \tag{D}$$

The average wave height at Crescent City during the first two hours of the tsunami is 85 cm. The calculation of the corresponding reflected wave height at Hanasaki is given in the table below:

(A) Wave height at 3,000 ft.,

$$H_{3000} = 85\left(\frac{20}{3000}\right)^{1/4} = 25 \text{ cm.}$$

(B) Height of wave reflected at 9,900 ft.,

$$H_R = 25\left(\frac{0.27}{1.27}\right) = 5.3 \text{ cm.}$$

(C) Wave height at 9,900 ft. off Hanasaki,

$$H_J = 5.3\left(\frac{1900}{6300}\right)^{1/3} = 3.6 \text{ cm.}$$

(D) Wave height at 20 ft. at Hanasaki,

$$H_H = 3.6\left(\frac{9900}{20}\right)^{1/4} = 17 \text{ cm.}$$

The travel time of the reflected wave from the Oregon Coast to Hanasaki is about 10 hours. The heights calculated in the above manner compare favorably with the average of the heights recorded at Hanasaki between 9 and 11 hours later (Fig. 9c). This close agreement is probably in part fortuitous, since many factors such as convergence and resonance have not been taken into account. The order of magnitude of the theoretical reflection coefficient, upon which the calculated height is critically dependent, seems to lead to agreement with this single set of observations.

The ratio between the average heights during the first 10 hours at Crescent City and the corresponding heights at Hanasaki remains nearly constant and serves to identify the waves at the two stations.

REFLECTION FROM CONTINENTAL SLOPES

Shepard (in press) gives 5° 20′ for the average slope and 10–20 mi. for the average range in width of the continental slopes bordering the Pacific Ocean. The depth at which the slope begins may vary from 600 to 3,000 ft. The present theory implies that the reflection coefficient at such average slopes is between 0.2 and 0.4 for normal incidence and between 0.15 and 0.3 for incidence at 45°. Thus, according to the theory, the reflected waves are of secondary but not negligible magnitude. At a given station, however, the reflected waves may be favored by convergence and be of primary magnitude. This might explain why the reflected waves are prominent only in relatively few cases.

REFLECTION FROM TRENCH WALLS

As pointed out above, the theory implies that a wave reaching a trench wall from shallower water is reflected totally if the angle of incidence exceeds a critical value. The arrival of the highest and most damaging waves at Napoopoo and Hokeena on the west coast of Hawaii about 18 hours after the April 1 earthquake (Shepard, *et al.*) can be explained by assuming that nearly total reflection occurred along the eastern edge of the Japan Trench and again at the Bonin Trench.

CONCLUSIONS

The data examined give good evidence that reflections do occur. One case has been subjected to quantitative treatment, and the observed wave heights were found to be in good agreement with those calculated on the basis of theory. The theory indicates that the reflected waves can be expected to be considerably smaller than the direct waves, except under very special circumstances. This conclusion is in agreement with observations.

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Contribution No. 378

A BIOCHEMICAL STUDY OF THE MARINE ANNELID WORM, *THORACOPHELIA MUCRONATA*

Its Food, Biochromes and Carotenoid Metabolism [1, 2]

By

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INTRODUCTION

Comparative biochemical studies of numerous marine invertebrates and fishes have indicated that the majority of such species so far examined selectively assimilate and store xanthophyllic or allied oxygenated carotenoids rather than carotenes, when consuming food containing both types of pigment. In some forms there is complete exclusion of carotenes, *e. g.*, in several fishes, in the sea mussel (*Mytilus californianus*), in at least three brittle stars, and in some color-variants of the anemone *Metridium senile.* Some asteroid echinoderms store carotenes, but in far lower concentrations than xanthophylls, while four species of echinoids appear to assimilate relatively greater quantities of carotenes (Fox, Updegraff and Novelli, 1944).

The marine polychaete worm *Thoracophelia mucronata* represents a metabolic departure from the above groups, since, while consuming a basic diet of finely particulate marine detritus similar to that ingested by mussels, brittle stars and sand dollars, it apparently stores only the carotene type (Sumner and Fox, 1933; Fox, 1936) and seems to destroy much of the xanthophyllic material. This is in direct contrast to *Mytilus* (Scheer, 1940) and to the ophiuroids *Ophiopteris papillosa, Ophiothrix spiculata* and *O. rudis,* which store xanthophylls but not carotenes (Fox and Scheer, 1941). *Thoracophelia* also exhibits more complete xanthophyll exclusion than does the sand dollar, *Dendraster*

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excentricus, for example, whose body carotenoids are some 24% xanthophylls. Other echinoids likewise exhibit a comparable preponderance of carotenes (Fox and Scheer, 1941).

Reference should be made also to the sponges. For while these must ingest much organic detritus, certain of them further resemble *Thoracophelia* in assimilating carotenes with relative exclusion of xanthophylls. *Suberites domuncula* and *Ficulina ficus* seem to yield no acidogenic carotenoids, questionable amounts of xanthophylls and large quantities of persistently epiphasic carotenoids with spectra resembling those of torulene, lycopene (*in Suberites*), α-, β-, and γ-carotenes (Lederer, 1938). The red sponge *Hymeniacidon sanguineum* was found to contain α-, β-, and γ-carotenes, as well as the ketonic carotenoid echinenone, more commonly encountered in sea urchins (Drum and O'Connor, 1940; Drumm, O'Connor and Renouf, 1945).

Because of its vast numbers, *Thoracophelia mucronata* is an undoubted factor in the physical and chemical turnover of organic matter on local sandy shores, in a manner somewhat analogous to the function of earthworms in terrestrial soils. Furthermore, this species has long served, and is still employed, as an important and economical source of food for experimental marine animals, including some collections maintained upon diets designed to provide carotene. Finally, the species constitutes an interesting case of an unusual biochemical ability—that of absorbing only carotene, with seemingly complete exclusion of xanthophylls. For the above reasons, and with improved methods and equipment available, it was decided to reinvestigate the pigments of *Thoracophelia* and their metabolism in a more searching manner than was previously possible.

GENERAL DESCRIPTION AND HABITAT

Thoracophelia mucronata is a blood-red worm of some 0.5 to 2.0 mm. in diameter and from about 30 to 50 mm. or more in length when mature. Sexes are separate. Adults examined in May, July and September contained ripe eggs and sperm. The animals live buried in intertidal sand, where they may be dug in large and concentrated numbers from a fraction of an inch to a foot or more beneath the sand surface during low or medium tides. The worms swallow much sand, readily seen to constitute the gut-contents and feces of freshly collected specimens. When collected in their wet sand and placed on damp paper or in sea water, the worms crawl out of the sand in a few hours, clearing their bodies externally and partially internally of sand and other detritus, thus preparing themselves for analysis.

Sand grains in the gut of the worm and in its feces do not differ significantly in size or appearance from the grains of the general environment; minute algal cells and detrital matter may be observed on the surface of such grains. The worms' biology, food and migrations within the sand constitute the subject of a separate research project.

The bright red and purplish colors of the worms are due to the presence of hemoglobin, which is not enclosed in erythrocytes, but is free in colloidal solution. The shed blood of this species was not observed to clot on exposure to air. Oxyhemoglobin was identified by its two characteristic sharp absorption bands, centering at 576 and 540 mμ respectively. Reduction with sodium hydrosulphite gave the single broad band of hemoglobin at 565 mμ (Hartridge reversion spectroscope). A strong positive test for hemoglobin was obtained with the benzidine reaction.

CAROTENOIDS AND CHROMOLIPOIDS

Methods. The worms were usually permitted the minimum interval of an overnight period in which to emerge and clear their bodies largely of sand and detritus. And, since we wished to minimize both incomplete digestive changes and aberrant post-mortem bacterial operations, final procedures sometimes involved the tedious step of hand-picking the emerged survivors. After blotting on towels, masses of the animals were weighted and comminuted to a fine mush under acetone in a blender.

Carotenoids were analyzed in accordance with regular methods applied to animal tissues (cf. Fox and Pantin, 1941). Exhaustive acetone extracts of the ground tissues were pooled, transferred to petroleum ether by dilution and extraction, then partitioned into epiphasic fractions (remaining in the petroleum ether phase) and hypophasic portions (migrating into the 90% methanol layer below). Epiphasic fractions were treated separately with warm alcoholic NaOH and subsequently repartitioned. Petroleum ether solutions of the final epiphasic and hypophasic pigments were separately washed, dried with solid NaCl and chromatographed. Samples of whole pigment extracts or of various separated fractions were examined spectroscopically in CS_2 or in "Skellysolve B," a refined hydrocarbon boiling between 60° and 70° C.

Skellysolve solutions of the pigments were chromatographed on Tswett columns consisting of MgO mixed with Hyflo Supercel (2 : 1 by weight) overlaid by similar columns of $CaCO_3$—Supercel mixtures of like proportions. The only colored zones from either epiphasic or hypophasic pigments were formed in the MgO portions of such columns.

Carotenoid material was measured in mg. per 100 g. of sand (dry basis) or worms (wet), with the use of a Bausch and Lomb spectrophotometer, the absorption of light at 485 mμ by CS_2 solutions of pigment giving values in β-carotene equivalents. It is to be remembered, however, that recorded determinations may depart from true values, since we were dealing with lipoidally contaminated extracts rather than with solutions of pure carotenoids.

Results. Samples of sand, containing none of the worms, but from the same environment, were analyzed for pigments. The first 3.5 kg. sample yielded approximately 0.06 mg. of collective xanthophylls (in "lutein" units) per 100 g. of sand on the dry basis. The xanthophylls were accompanied by unmeasured amounts of carotenes, probable chlorophylls and greenish degradation products of the latter. A second sample of sand from the environment of a worm colony was given more thorough study. It weighed 4.1 kg. when dried, and contained 0.70% of organic matter (by combustion). Extracts of the fresh, undried sand yielded the following approximate quantities of biochromes, separated by partition and chromatography:

Epiphase	*In whole sand (mg. per 100 g.)*	*In organic matter of sand (mg. per 100 g.)*
"Chlorophyll"	0.041	5.85
"Phaeophytin"	0.016	2.30
β-carotene	0.002	0.28
α-carotene	0.001	0.14
Hypophase		
Green breakdown products (in "chlorophyll" units)	0.025	3.60
Total carotenoids (*i. e.*, five xanthophyllic fractions, preponderantly fucoxanthins, with chief maxima at 508–510 and 477 mμ in CS_2)	0.064	9.04

It is observed that β-carotene occurred in twice the concentration of the α-isomer, and that collective xanthophylls constituted 95.5% of the total carotenoids.

While actual amounts and ratios of the pigments in the sand vary with locality, depth and season, this general condition is characteristic of fresh, mixed marine detritus, and lends emphasis to the biochemically selective behavior of the worm, which selectively stores the β-carotene, eliminates the α-carotene, and apparently destroys the xanthophylls at least in part.

TABLE I. CAROTENOID AND CHROMOLIPOID MATERIALS IN *Thoracophelia mucronata*

Sample	*History*	*Weight* (*g.*)	*Total extract* (*mg. %*)	*Total epiphasic material* (*mg. %*)	*Total xanthophyllic material* (*mg. %*)	*Carotene (from hydrolysate)* (*mg. %*)
I	Recently collected, but some dead included. Crude extract hydrolyzed.	218.7	——	——	0.01 (with chromolipoids)	0.15
II	Recently collected but some dead included.	75.5	0.30	0.24	0.01 (with chromolipoids)	0.215
III	Blood only, from freshly collected worms.	12 ml.	0.11	——	none (only chromolipoids)	0.04
IV	Collected previous day. Only live worms used.	75.5	0.25	0.18	none (only chromolipoids)	0.11
V	Starved one week in clean gravel and running, filtered sea water at 20° C.; only surviving worms used.	35.6	0.315	0.24	0.015 (with chromolipoids)	0.12
VI	Collected, washed and immersed in acetone within 3 hours.*	57.9	0.50	0.36*	0.01 (with chromolipoids)	0.24

* This extract contained some α-carotene (*i. e.*, about 13% of the total carotenes, the other 87% being β-carotene) due to the presence of undigested food residues in the gut, since the animals were purposely analyzed while the gut was still filled with sand.

That extracellular chlorophylls and xanthophylls are largely or completely decomposed in the gut of the worm was indicated first by analyzing fresh worms within three hours of collecting them, when their alimentary tracts still contained considerable sand, and second by a preliminary analysis of about 11 g. of sand voided by previously washed and segregated worms.

It will be noted (Table I, Sample VI) that there was an increase in the average amount of total extracted yellow pigment and of β-carotene itself in the fresh worms. Furthermore, traces of α-carotene were encountered, doubtless derived from the intestinal contents of the fresh sample. But no significant quantities of xanthophylls were observed.

The concentrated extract of the fecal sand was yellow, rather than green, in contrast to extracts of the fresh sand. On a chromatogram it yielded small amounts of chlorophyll-degradation products, carotene in a concentration of the same order of magnitude as that encountered in fresh sand (*i. e.*, 0.004 mg. per 100 g. sand) and, on the $CaCO_3$ portion of the column, no xanthophylls, but some yellow pigment which may have been derived from xanthophyll. It was hypophasic, but gave no positive tests for carotenoid material either with $SbCl_3$ or with concentrated H_2SO_4; furthermore, its absorption spectrum in CS_2 (Beckman instrument) showed maxima displaced farther toward the violet than those of fucoxanthin, their centers lying at 441 and 474 mμ, with a slight inflection at 498 to 499 mμ. While it would thus seem that fucoxanthins were destroyed in the gut of the worm, the bare possibility has not been excluded that such carotenoids may be desorbed from the sand (while β-carotene is not) and discharged in fluid feces.

The worms' bodies yielded yellow pigments which were chiefly epiphasic. The only consistently encountered carotenoid was a persistently epiphasic, alkali-resisting carotene whose absorption maxima were found to agree with those of β-carotene from plant sources, *i. e.*, 427–430, 450, and 476 mμ in Skellysolve (Fig. 1). The identity of the *Thoracophelia* pigments fraction with β-carotene was further confirmed by the results of the three-tube mixed chromatogram method: (1) β-carotene; (2) worm carotene; (3) a mixture of these two; in each of the three Tswett columns of MgO there appeared a single, identical orange zone of adsorbed pigment. Traces of more readily adsorbed pigments usually appeared on primary chromatograms of the persistently epiphasic fraction. Such material probably represented artifactual isomers, colored degradation products or other contaminants. But no α-carotene, which accompanies the β-isomer in this and all other marine sediments and commonly appears as a yellow zone be-

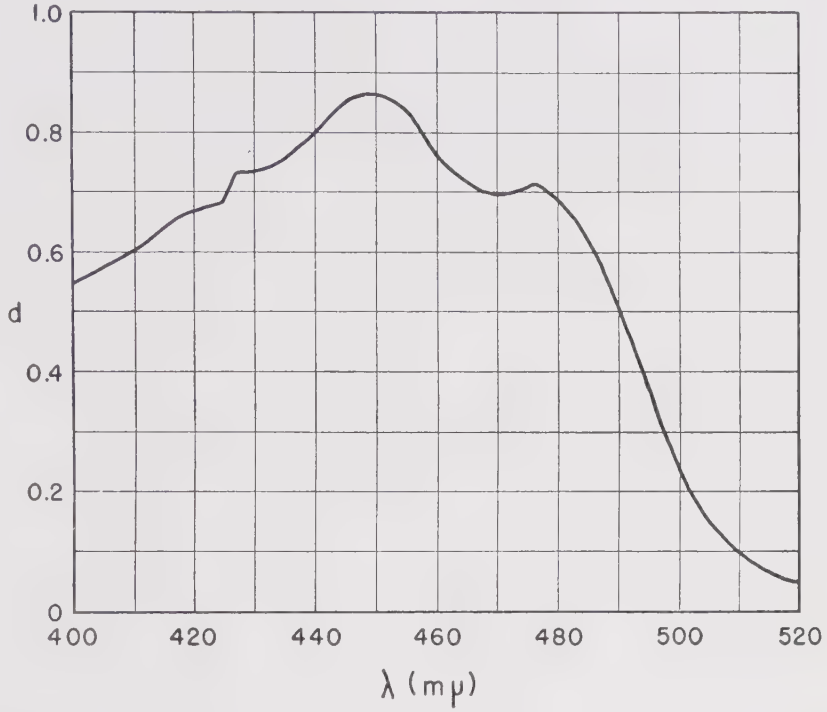

Figure 1. Absorption curve (Beckman) of β-carotene from *Thoracophelia*. Solvent Skellysolve B.

neath the orange band of the latter, was ever detected in extracts of the worm, save in traces when extracts were prepared from the fresh, actively feeding animals (Table I, Sample VI). The worm's assimilation of β-carotene, while excluding or destroying not only xanthophylls but even the isomeric α-carotene, all of which occur in the natural diet (Fox, *et al.*, 1944), seems remarkable. Quantitative spectrophotometric estimations of carotene in the worms' tissues are summarized in Table I.

The total yellow pigment values of 0.30, 0.25, 0.315, and 0.50 mg. %, measured as β-carotene equivalents on the raw extracts, agree rather well with that of 0.38 mg. % found earlier by a less refined, nonspectroscopic photometric method (Sumner and Fox, 1933).

Both epiphasic and hypophasic fractions yielded small amounts of yellow noncarotenoids which exhibited properties characteristic of the so-called chromolipoids or lipofuscines. Such pigments passed unadsorbed through $CaCO_3$, but could be chromatographed on MgO columns. More of this material was hypophasic than epiphasic. Most of the chromolipoid pigment which was initially epiphasic could be rendered hypophasic by treatment with alcoholic NaOH. A common property of the various fractions was the manifestation of blue fluorescence when dissolved in Skellysolve and illuminated with the beam of a carbon arc or with light through an ultraviolet filter. These

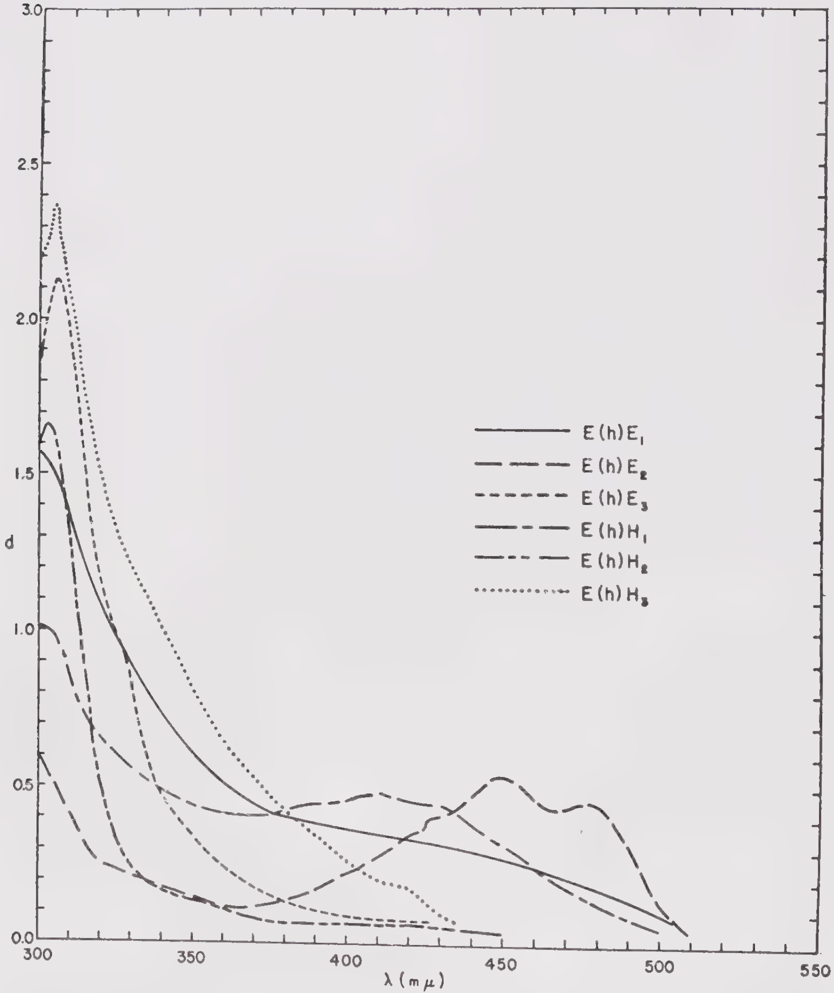

Figure 2. Absorption spectra (Beckman) of the persistently and initially epiphasic pigment (β-carotene and chromolipoids) from *Thoracophelia*. Solvent: Skellysolve B. Lettered fractions as in Table II.

chromolipoids were readily distinguishable from carotenoids by their fluorescent properties, by their absorption spectra, and by their failure to exhibit blue or green colors, showing instead brown, brown-yellow or brown-orange when treated with concentrated H_2SO_4. Chief among these distinguishing characters were the absorption spectra (Figs. 2, 3), which showed only slight absorption in the blue-green, blue

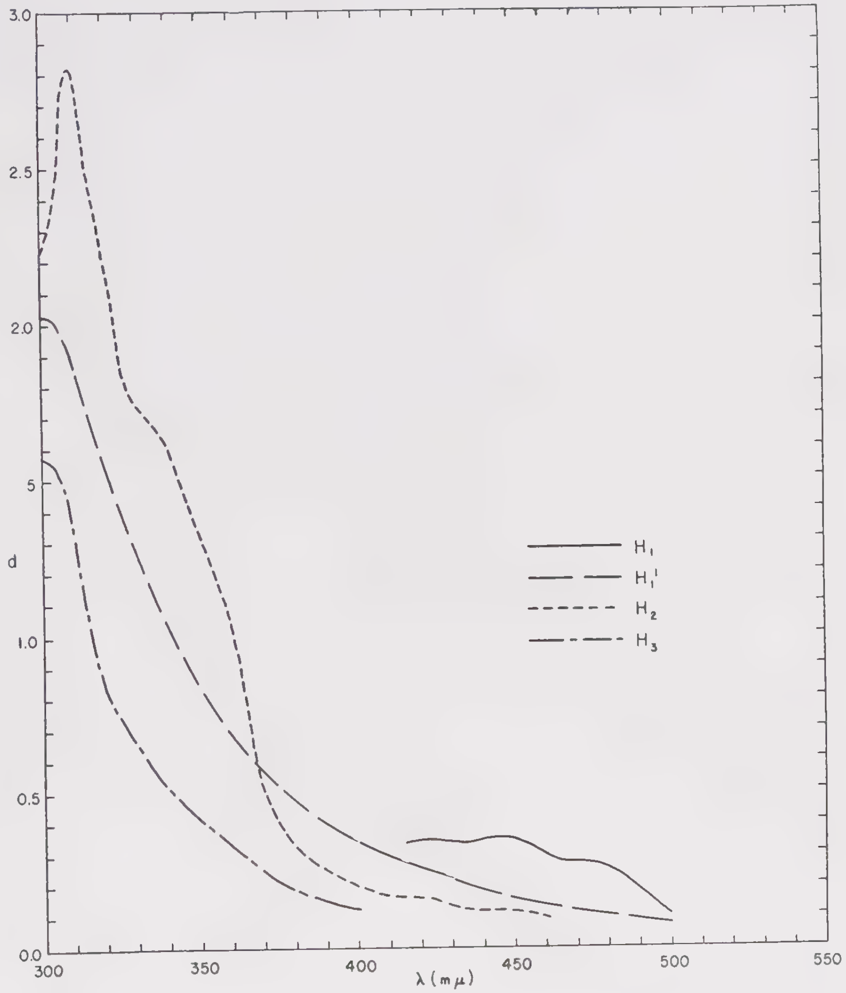

Figure 3. Absorption spectra (Beckman) of the hypophasic chromolipoids of *Thoracophelia*. Solvent: Skellysolve B. Lettered fractions as in Table II.

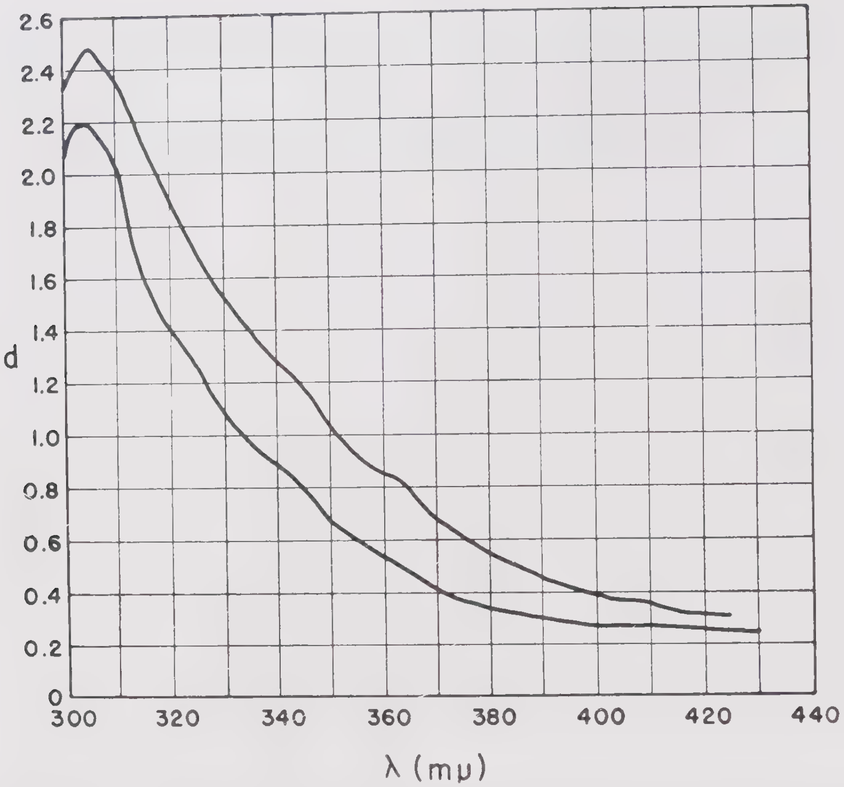

Figure 4. Comparative absorption spectra of a hypophasic chromolipoid (upper curve) and an apparently identical fraction derived by hydrolysis of an originally epiphasic, presumable ester (lower curve). Beckman instrument. Solvent: Skellysolve B.

and blue-violet but which demonstrated steeply rising absorption in the violet, often with a sharp maximum at values from 300 to 310 mμ. Similar absorption curves of some initially hypophasic fractions, and of originally epiphasic ones rendered hypophasic by hydrolysis, suggest the presence in the tissues of a free and an esterified alcoholic component of some kind (Fig. 4). The absence of colored insoluble carotenoid salts at the interface of diluted alcohol-NaOH hydrolysates and petroleum ether indicated the absence, from either epiphasic or hypophasic extracts, of any acidogenic carotenoids commonly encountered in crustaceans, echinoderms, coelenterates and mollusks.

Treatment of the chromolipoid fractions with $SbCl_3$ in $CHCl_3$ solution failed to show the blue colors which characterize Vitamin A and numerous colored carotenoids, but resulted instead in pink to mauve colors. The absorption spectra, color of fluorescence, and hypophasic behavior of our chromolipoid fractions eliminate any identity with phytofluene, the widely occurring plant polyene hydrocarbon described by Zechmeister and Sandoval (1946). While the Liebermann-Burchard reaction demonstrated the presence of sterols in a number of the fractions, it is not believed that such compounds were responsible for the yellow color, since some yellow fractions seemed to contain no sterols, and since the better known sterols are colorless, absorbing light only in the ultraviolet range.

It is of interest to note, however, that the great majority of the chromolipoids were apparently neutral compounds. Two fractions only, H_1' and $E(h)E_1$, were not eluted by neutral acetone or acetone-Skellysolve systems, but could be removed from the MgO after acidification of the eluant with acetic acid. Therefore, these two portions may have had acidic properties, while the behavior of the others suggests higher alcohols.

Information relative to the lipofuscine fractions separated from sample V is summarized in Table II.

Four out of six lots of worms analyzed yielded traces of a hypophasic xanthophyll-like component or degradation product. This fraction departed from typical xanthophyllic behavior in that it passed through $CaCO_3$ Tswett columns unadsorbed. But it was adsorbed as a pink zone above the fluorescent noncarotenoid on the MgO portion of the column. Absorption maxima in CS_2 lay between 475–485 mμ and 505–510 mμ (Bausch and Lomb visual spectrophotometer) and in Skellysolve at 422–425, 446 and 472 mμ (Beckman photoelectric instrument). Such values are reminiscent of those of lutein (420, 446.5, 476 mμ in petroleum ether or ethanol) and taraxanthin (417, 443, 472 mμ in ethanol), but are not identical with either set of values. No such material was recovered from hydrolysates of epiphasic fractions. Because of its inconsistent occurrence, the minute traces in which it was found when present, its atypical chromatographic behavior and the fact that no corresponding esters were ever found, we believe that this pigment may reflect either the decomposition of carotene or the presence of undegenerated food-residues in the intestinal tract of the animal. The inadsorbability of any yellow *Thoracophelia* pigments on $CaCO_3$ had been observed in the earlier work of Sumner and Fox (1935).

In its prevention of xanthophylls from entering the system, whether by not permitting diffusion through the intestinal mucosa or by destruction of such pigments in the lumen of the gut, *Thoracophelia* resembles some higher herbivores or omnivores rather than many of the lower forms. Cattle are known to absorb a part of the dietary

TABLE II. PHYSICAL AND CHEMICAL PROPERTIES OF CHROMATOGRAPHIC PIGMENT FRACTIONS FROM *Thoracophelia*

Fraction (*color on* MgO *column*)	*Blue fluorescence*	*Absorption max.* (*m*μ)	SbCl$_3$ *reaction*	*Liebermann-Burchard reaction for sterols*		*Acid treatment*	
				H$_2$SO$_4$ *layer*	CHCl$_3$ *layer*	H$_2$SO$_4$ *layer*	CHCl$_3$ *layer*
H_1 (pink)	+	<300	pink	purple	green	....	....
H_1' (pink)	+	ca. 300; 423; 446; 472	murky	brick-red	brown	....	....
H_2 (purplish-gray)	+	310 (sharp)	red-orange	purple	blue-green	....	....
H_3 (no colored zone)	+	ca. 300	pink (±)	faint purple	pale yellow	....	....
$E(h)E_1$ (orange)	+	<300	pale pink	purple	blue-green	....	....
$E(h)E_2$ (orange)	+ (impurity)	(427); 450; 477 (β-carotene)	blue	green or purple	colorless to blue	green	brown (impurities)
$E(h)E_3$ (diffuse yellow)	+	306 (sharp)	pink (±)	purple	brown	....	....
$E(h)H_1$ (reddish)	(+)	ca. 300; (390); (410); (428)	–	–	–	pale brown	bleached
$E(h)H_2$ (yellow)	(+)	302.5 (sharp)	–	–	–	pale yellow-brown	bleached
$E(h)H_3$ (yellow filtrate)	(+)	305 (sharp)	pink	deep blue	green	orange	brown-orange

H = hypophasic pigment
E = epiphasic pigment
(h) = hydrolytic operation
$E(h)E$ = persistently epiphasic pigment
$E(h)H$ = originally epiphasic pigment rendered hypophasic by hydrolysis.

Subscript numbers refer to chromatographic position, beginning at top.

H_1' = fraction of H, elutable with acetic acid; similarly with $E(h)E_1$.
(+) = very faint positive
± = questionable
– = no reaction detected.

Maxima recorded in parentheses indicate very weak ones or points of inflection.

carotenes but very little xanthophyllic compounds (Palmer and Eckles, 1914; Goodwin, Dewar and Gregory, 1946). Sheep store mere traces of carotene and Vitamin A in their blood and other tissues (Palmer, 1916; Paulsen, Hilmoe and Moxon, 1944; Peirce, 1945) while excreting in their feces 70% of ingested carotenes and 80% of the xanthophylls consumed (Rogozinski, 1937). Vitamin A introduced by abdominal cannula into the digestive tract of sheep and goats produces a rise of Vitamin A levels in both systemic and portal blood, but colored carotenoids so introduced are not reflected in the blood in this way (Goodwin, *et al.*, 1946). It is believed that sheep must destroy xanthophylls in the digestive tract (Rogozinski, 1937). The same view is held regarding the horse, which assimilates only carotenes from green food, but excretes 70–80% of the dietary carotenes and 60% of the xanthophylls ingested. Since none of the latter are assimilated as such, they must be partially destroyed in the gut (Zechmeister and Tuzson, 1934; Zechmeister, Tuzson and Ernst, 1935). Hove (1943) found that water-extracts of minced rat stomachs destroyed carotene rapidly in vitro, in the presence of methyl linolate. He suggests the possible presence of carotene oxidase or lipoxidases. Sherman (1947) has shown that gastro-intestinal destruction of dietary carotene in the rat may be decreased by the administration of lutein. He suggests that the effect of the lutein may be due to its preferential destruction by a nonspecific enzyme which may be responsible for the degradation of carotenoids generally. The cod, *Gadus callarias*, and the lobster, *Homarus americanus*, are believed to slowly convert carotene into Vitamin A, as do mammals and birds (Neilands, 1947; Mattson, *et al.*, 1947; Wiese, *et al.*, 1947).

No destruction of xanthophylls from sand were demonstrable in preliminary experiments involving the incubation of such material (adsorbed in $CaCO_3$) with pastes of ground *Thoracophelia*. Partially starved worms (Table I, Sample V) exhibited no significant changes in carotene content, but did show slightly elevated quantities of the yellow noncarotenoid chromolipoid material (absorption at 305 mμ about 3 : 1).

In its assimilation of β-carotene without the accompanying α-isomer, *Thoracophelia* seems to be unique. This finding is contrary to an earlier provisional conclusion that the carotene in this species was preponderantly the α-isomer (Fox, 1936).

The reinvestigation of carotenoids in *Thoracophelia* lends emphasis to a provisional conclusion reached earlier by Sumner and Fox (1935) regarding the probable conversion of carotene into xanthophyll by the Pacific killifish, *Fundulus parvipinnis*, which stores only esterified members of the latter class. Fishes maintained for three months upon carotenoid-free food neither lost nor gained xanthophyll, while parallel groups fed upon xanthophyll-rich flesh, and those kept on a diet of *Thoracophelia* underwent increases in total amounts of stored xanthophyll. Chemical examinations made at the time of those experiments and subsequently (Fox, 1936) revealed none of the yellow noncarotenoid chromolipoids of *Thoracophelia* in the fishes which ate the worms, since hydrolyzed extracts of the fish pigments were quantitatively adsorbed upon $CaCO_3$ columns and exhibited well defined absorption spectra.

Nor could the increase of xanthophyll stored by the worm-fed fishes have been logically assigned to the traces of "xanthophyll" sometimes encountered in the worms, for the average amount of residual "xanthophyll" revealed by the present survey is, according to Table I, about 0.031 mg. from the collective 475.2 g. of worms, or some 0.006 mg. % on the average. Sumner and Fox (1935) fed their worm-eating lot of *Fundulus* about 2000 g. of this food, corresponding to roughly 0.12 mg. of "xanthophylls" (and 6 mg. of carotene) over the three month experimental period. During that interval the growing consumers, while undergoing a decrease in *concentration* of stored xanthophylls, nevertheless achieved an actual collective augmentation of approximately 0.20 mg. of this class of carotenoid. Even quantitative absorption of all available dietary xanthophyll (which is not known to occur in any animal, and certainly was not achieved by the xanthophyll-fed lot in the experiment cited) would have fallen 40% short of supplying the observed increment. Since synthesis of xanthophylls from colorless precursors did not appear to take place in the fishes receiving the carotenoid-free diet of halibut flesh, we are still left with the conclusion that *Fundulus* must be able to convert nonxanthophyllic into xanthophyllic carotenoids. Furthermore, the only carotenoid which the fishes could have received from *Thoracophelia* was β-carotene.

COMPOSITION, FOOD AND METABOLISM

The finding in the worm's gut of little else of a microscopically visible nature save sand grains led to a consideration of the basic food of the animal.

The gut wall consists of deep and multiple longitudinal folds throughout its anterior portion and is provided throughout its length with rapidly sweeping cilia upon its inner surfaces. Peristalsis is marked. These factors, added to the rich blood supply in the intestinal walls, provide for intimate contact with the ingested sand grains in the region of digestion and absorption.

Beyond question, the organic material present in the sand exists largely as adsorbed colloidal micelles and other fine particles. This adsorptive property of sand, which had previously been chemically cleaned, was demonstrated in the laboratory by gentle agitation with colloidal material prepared by the fine comminution of marine plants, followed by centrifugal removal of the coarser particles. Extraction of the treated and subsequently water-rinsed sand with acetone yielded green and yellow plant pigments. Egg albumin, the colloidal dye congo red, and the crystalloid organic dyes night blue, methyl violet and methylene blue were also observed to be readily and firmly adsorbed to sand. Congo red was adsorbed more readily to raw, untreated sand, wherefrom it could be removed incompletely and with difficulty by vigorous shaking, while the other dyes became adsorbed in greater quantities to the previously cleaned sand. These observations suggested that the marine organic colloids already adsorbed upon the raw sand must inhibit somewhat the additional adsorption of crystalloidal dyes, while increasing that of the electrically charged colloid dye congo red.

Use was made of the firm adsorbability of the nontoxic dye, methylene blue, upon sand to demonstrate the approximate rate of sand-ingestion by the worms. The dyed sand was washed with sea water until no further dye was thus desorbed and washed out, but still leaving the sand a deep blue color. Freshly collected *Thoracophelia* were then buried in the damp blue sand contained in earthenware plant-pots, standing partially immersed in sea water. Subsequent examination disclosed that numerous specimens had evacuated the raw sand from the gut and had replaced this with the dyed sand within 15-minute intervals. The dyed sand was in turn readily replaced by normal sand when the worms were given the opportunity. They seem to swallow either substrate equally readily.

The proportions of water, ash and total organic matter in fresh worms were determined, as well as the relative quantities of sand which had been ingested (all as listed in Table III). The values for sand were determined by treatment of the ash with dilute HCl, followed by reweighing the dried insoluble residue. The results obtained are doubtless conservative, since carbonates and iron sulfide are soluble in dilute acids and therefore would have been removed by the treatment accorded the ash.

Some rough calculations may be useful in suggesting the quantities of sand and organic matter adsorbed thereto, which the worms may ingest and utilize in order to build up or maintain the organic material of their tissues.

TABLE III. COMPOSITION OF FRESH WORMS CORRECTED FOR QUANTITIES OF INGESTED SAND (SILICA)

	Sample 1	*Sample 2*	*Average*
Wet weight, g.	40.97	37.33	.....
Dry matter, *corrected for silica,* %	19.82	19.70	19.76
Water (by difference), %	80.18	80.30	80.24
Ash, *corrected for silica,* %	2.02	2.02	2.02
Organic matter (by difference), %	17.80	17.68	17.74
Silica in gut (g. per 100 g. of fresh worm tissue)	5.84	5.29	5.56

The whole worms contain close to 18% organic matter and swallow some 6% of their own weight of sand. This sand may contain about 1% of organic matter, *i. e.*, by taking a rough average between our figure of 0.7% and the value of 0.1% of organic nitrogen (given by Revelle and Shepard, 1939), the latter value being multiplied by a factor of 14 to 18 to give the total organic matter (Trask, 1939). Thus, if 100 g. of the worms fill their alimentary tracts each quarter hour with 6 g. of sand, this represents a cycle of more than 210 kg. of sand per annum, or of somewhat more than 2000 g. of organic matter adsorbed to the sand. Grown specimens weigh about 40 mg. each and therefore ingest on the average some 9 mg. of sand per hour, 0.23 g. per day, or about 84 g. per year. Adult animals would appear to operate at a biochemical efficiency of 18/2000 x 100 or 0.9% during a year's time. And it is worth re-emphasizing that the worm, while assimilating none of the relatively plentiful xanthophylls or α-carotene from the organic matter in the sand, contrives to concentrate the β-carotene by some five-fold, if we take 0.28 mg. of β-carotene as its concentration in the organic matter of the sand and 100/18 x 0.25 or 1.4 mg. as its approximate concentration in the worm's organic matter.

Some approximate values are given in tabular form below, to indicate the relative magnitude of local operations of the beach-worm. Populations are based upon counts of samples, and values for the density of sand, the rate of its ingestion, etc., are based upon measurements of samples.

Volume of damp sand in worm-bed, 1 mile long, 10 ft. wide, 1 ft. thick	5.28×10^4 ft.^{3}
Weight of damp sand in this volume (density ca 131 lbs/ft.^{3})	3.46×10^3 tons
Weight of actual sand (subtracting ca 18.5% water)	2.82×10^3 tons
Total number of worms in worm-bed (ca 3×10^3/ft.^{3})	1.58×10^8
Total weight of worms in worm-bed (ca 0.04 g. each)	7.0 tons
Weight of sand cycled annually by worms (ca 84 g. each)	1.46×10^4 tons

Ratio of sand cycled annually by worms to sand in worm-bed $\frac{1.46 \times 10^4}{2.82 \times 10^3} = 5.2$

(equivalent to all the sand in the worm-bed about once every 10 weeks)

Organic matter in sand cycled annually by worms (ca 1%)...... 1.46×10^2 tons
Organic material in worms in the colony (ca 20%)............... 1.4 tons
Relative efficiency of worms in maintaining a standing population, assuming an annual life-cycle............... $\frac{1.4 \times 10^2}{1.46 \times 10^2} = 0.96\%$

Quantity of carotene in sand of worm-bed (ca $2.8 \times 10^{-4}\%$).......... 16 lbs.
Quantity of carotene in worms of the colony (ca $2.5 \times 10^{-4}\%$)........ 0.035 lbs.
Relative efficiency of carotene assimilation, assuming an annual life cycle.................................... $\frac{0.035 \times 10^2}{16 \times 5.2} = 0.042\%$

Volume of sand in wedge of beach, 1 mi. long, 200 ft. wide, 2.5 ft. high.. 1.32×10^6 ft.^{3}
Weight of dry sand in wedge.............................. 7.05×10^4 tons

Fraction of sand on beach cycled annually by worms..... $\frac{1.46 \times 10^4 \times 10^2}{7.05 \times 10^4} = 21\%$

SUMMARY

1. The blood-red, hemoglobin-containing, sand-eating marine polychaete worm, *Thoracophelia mucronata*, carries in its blood and other tissues appreciable quantities of β-carotene.

2. No α-carotene or other carotenoids could be detected in the worms' tissues, save for inconsistent traces of an unesterified, hypophasic, xanthophyll-like pigment or colored degradation product which was unadsorbed by $CaCO_3$.

3. Small quantities of yellow, noncarotenoid blue-fluorescent chromolipoids are extractable. Some of these are hypophasic initially, while others are rendered so by hydrolysis. These chromolipoids exhibit low light-absorption in the green, blue and blue-violet regions, but single sharp maxima in the ultraviolet at 310, 306, 305, 302.5, 300 mμ or below.

4. Although no carotenoid oxidase was demonstrated, it is suspected that the remarkable exclusion of xanthophylls from its system by *Thoracophelia* may be allied to the presence of lipoxidases, which must participate in the genesis of the animal's yellow chromolipoids.

5. *Thoracophelia* probably derives its subsistence from the colloidal organic matter adsorbed to the sand. Consuming some 24% of their own weight of sand per hour, 100 g. of the animals must ingest some 210 kg. of sand annually, representing about 2000 g. of organic matter. Since each adult worm weighs about 40 mg., this is equivalent to about 84 g. of sand (containing .84 g. organic matter) per worm per year.

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Contribution No. 379

CHANGES IN THE FISH FAUNA OF WESTERN NORTH AMERICA CORRELATED WITH CHANGES IN OCEAN TEMPERATURE[1]

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Many lines of evidence support the conclusion that temperature is a factor of prime importance in the distribution of marine fishes along the Pacific Coast of North America. The correlation between water temperature and the type of fish found is so definite that I feel justified in drawing inferences, from the known data of fish distribution, regarding ocean temperatures of the past and regarding the temperatures of regions for which the physical data are inadequate. Several patterns in the present distribution of fishes along the coast can be plausibly explained only on the theory that ocean temperatures fluctuated considerably, up and down, during recent geological time. Largely on the basis of warm-water forms reported from 1853 to 1860, I further infer that the ocean temperatures at that time, nearly one hundred years ago, were definitely higher in the southern half of California than they have been during any subsequent series of years.

Some call such two-way use of data unwarranted—a "vicious circle" —but I regard the method, when used with due caution and insight, as both proper and promising. Consistency in results and in explanations is a justification of the procedure. A similar approach was used in a recent correlation of hydrographic history and fish distribution in the Great Basin (Hubbs and Miller, 1948).

Even though I almost completely restrict the treatment zoologically to fishes, geographically to western North America, and temporally to the present and near-present, I must sail rapidly through a sea of extensive, varied and detailed data. In particular, the correlation between present temperatures and the present distribution must, for want of space, be treated sketchily. Chief emphasis in this paper is given to fish faunal changes associated with short-term (annual) and long-term changes in surface temperature within historic time.

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REVIEW OF ZOOGEOGRAPHICAL EVIDENCE

The general transition of the fish fauna from Arctic to Tropic waters along the Pacific Coast illustrates well the correlation between temperature and distribution. The relative sharpness of the change in temperature at Point Conception is reflected in the rather rapid transition there between the fish fauna of southern California, with a large representation of subtropical types, and that of central California, with many subarctic forms.

The correlation between temperature and distribution is especially emphasized where the latitudinal transition is locally reversed. Thus, the general southward increase in temperatures and the increasingly tropical aspect of the fauna is reversed in northwestern Baja California, from near the California border southward through at least 2.5° of latitude. Here the offshore temperatures during the critical spring and summer months may run 1° C. cooler than near San Diego (according to unpublished data assembled under the direction of George F. McEwen). More significantly, the inshore temperatures of this region are in general unusually low, very strikingly so in foci of upwelling (McEwen, 1916). The validity of the areas of upwelling charted by McEwen (his plate 9) is being confirmed by recent data. Thus on August 8, 1948, the temperature of the surf was only 15.1° C. at or near the focus of the area of upwelling just south of the border, only 13.6° at Santo Tomás Anchorage south of Ensenada, and generally low in the intervening areas, except in Todos Santos Bay, where partial enclosure and shallow water produce a warm area, with temperatures on August 8 as high as 22.6° (at a point only 13 nautical miles north of Santo Tomás Anchorage). Furthermore, due to the prevalence of upwelling and the general lack of eddies, the temperatures off most of the coast of northwestern Baja California (Todos Santos and Sebastian Viscaino Bays excepted) can not be expected to attain the occasional heights experienced in southern California (as Harald U. Sverdrup pointed out in discussing this problem). In striking agreement with the oceanographic conditions, we are finding south of the international border, in the areas of upwelling, a very considerable representation of central California fish types. Some of the species, for instance the reef seaperch, *Amphigonopterus aurora*, appear to have a discontinuous range, broken in southern California and probably also in such warm areas of Baja California as Todos Santos Bay. Other fishes and some invertebrates (as the red abalone, *Haliotis rufescens*, and the large sea urchin *Strongylocentrotus franciscanus*) that occur near San Diego only in the cooler infratidal waters reappear between tides in the areas of upwelling in Baja California. Other species occur in shallower water in those areas. A strikingly parallel picture of algal distribution in northwestern Baja California has been discovered by E. Yale Dawson (personal communication). Our findings have been given brief advance notice, as by Hubbs (1946: 84), Barnhart and Hubbs (1946: 371) and Stephenson and Stephenson (1948: 7).

The prevalence along the Oregon and Washington coasts of upwelling, which lowers the inshore surface temperatures, seems to be associated with the absence there of certain fishes, such as the Californian reef klipfishes *Gibbonsia montereyensis* and *G. metzi*, that reappear in British Columbia. Other southern fishes that occur in British Columbia are listed by Clemens and Wilby (1946: 4). The extremely cold water just south of Monterey Bay is correlated with the occurrence there of such northern reef fishes as *Scytalina cerdale, Phytichthys chirus, Artedius harringtoni* and *Clinocottus embryum.*

Warmer bays have a far more southern fauna than the adjacent open coast. Thus we note the occurrence of a southern pipefish, *Syngnathus arcta*, and the abundance of the least seaperch, *Micrometrus minimus*, and of a southern flatfish, *Hypsopsetta guttulata*, in Elkhorn Slough and Tomales Bay, central California. Morro Bay has a particularly southern fauna, in harmony with the warmth of its waters, caused by the extensive shoals of blackish mud. Here occur the California killifish, *Fundulus parvipinnis*, otherwise seemingly absent north of Santa Barbara, the southern California subspecies of the staghorn sculpin, *Leptocottus armatus*, and the northernmost population of the pipefish *Syngnathus griseo-lineata leptorhyncha*, separated from the main range of this subspecies by another subspecies, *S. g. barbarae.*

The along-shore cooling effects of upwelling in Oregon and Washington are strikingly evident in the southward extension of the range of many subarctic fishes. Farther offshore, beyond the effects of upwelling, occur fishes of more southern types, such as the mola (*Mola mola*), albacore (*Germo alalunga*), bluefin tuna (*Thunnus thynnus*), and more southern types of sharks.

In the cases of more or less isothermal bathymetric distribution, the effect of temperature transcends that of light and a great variety of other factors. Thus certain forms that inhabit intertidal reefs in central California occur in the cooler infratidal waters in southern California. Examples are a klipfish, *Gibbonsia montereyensis*, and a rockfish, *Sebastodes chrysomelas.* Like the two invertebrates mentioned previously (*Haliotis rufescens* and *Strongylocentrotus franciscanus*), these two species reappear on certain intertidal reefs of Baja California where the water is unusually cool. A midshipman, *Porichthys notatus*, breeds in intertidal waters in central California but not in southern California. In general, fishes of wide latitudinal distribution occur in deeper water to the southward. Thus the ratfish, *Hydrolagus colliei*, lives close to shore in Puget Sound, but chiefly in about 50 to 100 fathoms near San Diego. The seven-gill cowshark (*Heptranchias maculatus*) is common in the shallow parts of San Francisco Bay, but off San Diego it is taken chiefly off the open coast at depths of about 50 fathoms. A rockfish, *Sebastodes mystinus*, abounds in central California close to the rocky shores and near the surface offshore, but is confined in southern California to rather deep water. It is hoped that supporting data will be marshalled in future publications.

The seasonal movements of fishes along the coast are clearly controlled by water temperatures. Thus marlin, *Tetrapturus mitsukurii*, do not appear off San Diego until or unless the surface temperatures approximate 70° F. Albacore, *Germo alalunga*, are looked for at temperatures approximating 60 to 65° F. The wide movements of the sardine, *Sardinops caerulea*, are also definitely seasonal.

Though the data have been presented so sketchily and though much of the detailed information remains to be gathered and collated, it seems safe to assert that the distribution of marine fishes along the Pacific Coast of North America is determined to a large degree by the sea temperatures. This assertion, of course, is bolstered by the close relations between temperature and distribution established for fishes in other parts of the world, and for other groups of organisms.

INFERENCES FROM FAUNAL EVIDENCE REGARDING PREHISTORIC CHANGES IN SEA TEMPERATURE

On the basis of present distribution it may be inferred that isotherms and fish faunas have been displaced both northward and southward during recent geological time. Unhappily the Pleistocene fish faunas are much too poorly known to bring to bear on this problem, in the way that warm-water and cool-water Pleistocene mollusk faunas have been cited to indicate such thermal and faunal shifts (Smith, 1919; Schenck and Keen, 1937; etc.).

The evidence for past northward shifts in ocean isotherms and fish distribution is found chiefly in the occurrence of southern forms northward, in appropriate waters beyond discontinuities in distribution. Reference has been made already to the occurrence in British Columbia of certain Californian fishes that do not live in the intervening cool regions of maximum upwelling; also, to the northern outliers of southern types in certain warmish bays, particularly Morro Bay. Since none of the southern relicts shows any evidence of differentiation, the past connections, probably during periods of warm climate, were presumably in late Quaternary time. The warm Postglacial period, generally recognized on the basis of pollen profiles and other evidence, suggests itself as the time when isotherms and fish faunas were displaced northward along the coast.

A small body of fish evidence and a larger amount of mollusk data from Indian kitchen middens support the view that displacements both northward and southward have taken place during Postglacial times.

The occurrence along the northwestern coast of Baja California of northern coastal relicts, likewise undifferentiated, may be taken to indicate a very late Pleistocene or early Recent southward displacement of isotherms and fish faunas. The presence of a rainbow trout, *Salmo gairdnerii nelsoni*, in certain streams of the region has been thought of as confirmatory evidence of such a southward shift, but the inference is not secure (Hubbs, 1946: 85), not nearly so convincing as the inference for past displacements that can be drawn from the presence in Formosa (Jordan and Oshima, 1919: 122; Jordan and McGregor, 1925: 137) of a land-locked salmon (*Oncorhynchus formosanus*).

A more ancient and more extensive southward displacement of isotherms and faunas is indicated by the occurrence of a rather large number of northern relicts in the upper part of the Gulf of California, where the summer water temperatures are high and the winter temperatures low. The types with northern affinities coexist with a somewhat depauperate Panamaic fish fauna. Most of the northern Gulf relicts and their respective Californian cognates do not now range into the almost strictly tropical waters about Cape San Lucas. The connection presumably existed at some ancient time, or more probably at several times. Since, according to published and unpublished studies, the level of differentiation grades from full-specific to racial or none—usually weakly specific or subspecific—and since southward displacements are generally accepted as having occurred during the Glacial periods, it seems logical to date the connection or connections as Pleistocene. The occurrence of a specifically differentiated trout of the *Salmo gairdnerii* series in the upper part of the Gila River system seems attributable to a similar displacement. Other northern fish relicts in various streams of the Pacific Coast drainage are probably also of Pleistocene derivation (data in part cited by Hubbs and Miller, 1948).

LONG-PERIOD NORTHWARD DISPLACEMENTS OF FISH FAUNAS WITHIN HISTORIC TIME

In agreement with other lines of evidence, data on changes in the distribution of fishes along the Pacific Coast suggest that climatic oscillations have persisted into historic time. There are strong indications that the ocean temperatures from 1850 (or earlier) to about 1870 were definitely warmer in the southern half of California than during subsequent decades, and there are weaker suggestions of a reverse change in temperature and fauna during the past two or three decades.

The fish fauna of San Diego, as sampled from 1853 to 1860, particularly by the Pacific Railroad Survey from 1853 to 1857 (Girard, 1858; etc.), was definitely more tropical than that of any subsequent decade. Of the 30 odd species reported, six (about 20%) do not now occur so far north or have been so rare recently that one certainly would not expect any to be caught at present by such incomplete and superficial collecting as that of the 1850's and 1860's. Possible sources of gross error have been disregarded after due consideration. The Pacific Railroad Survey secured at San Diego: five specimens of the giant seahorse, *Hippocampus ingens*, few of which were collected north of Magdalena Bay from then until 1880 and none since that year; four examples of a presumably tropical pipefish, *Dermatostethus punctipinne*, which has never been secured again, anywhere; several individuals of an unidentified triggerfish (of the tropical family Balistidae), which seemingly has not been collected again in the eastern Pacific; two spadefish, *Chaetodipterus zonatus*, of which the only subsequent California record is for a specimen taken in the extremely warm summer of 1931 (p. 467); a puffer, *Sphoeroides politus*, of which only one doubtful example has been secured in California since 1880 and few before that year; and a jack, *Caranx caballus*, of which single specimens have been reported from California in 1857, 1924, and 1945. The only northern species reported from San Diego by Girard was the seaperch *Taeniotoca lateralis*, but this species was represented by a single adult; this species ranges commonly south to the Santa Barbara Islands and it has been collected recently near San Pedro and in northern Baja California.

Nearly as impressive is the evidence that the fish fauna at Monterey during the first two decades of the second half of the nineteenth century was made up to a considerable degree of fishes now characteristic of the relatively warm waters south of Point Conception. Only about twenty species were reported from Monterey by the Pacific Railroad Survey, but the list includes five or six kinds that do not now occur so far north or are so rare as not to be collectable by any such dribbling survey as that of the 1850's. These southern types are the sand bass, *Paralabrax nebulifer*, the California sculpin, *Scorpaena guttata*, the bay blenny, *Hypsoblennius gentilis*, the garibaldi, *Hypsypops rubicunda*, the horned shark, *Heterodontus francisci*, and perhaps the guitarfish, *Rhinobatos productus* (recorded as from either Monterey or San Francisco). The evidence that the California flyingfish, *Cypselurus californicus*, occurred prior to 1864 north as far as Santa Cruz on Monterey Bay has been cited (Hubbs and Kampa, 1946: 209) as an example of former occurrence of southern forms north of their present range. As noted by Steinbeck and Ricketts (1941: 48) and by Schmitt (1921: 163), *Pleuroncodes planiceps*, a very conspicuous crustacean that swarms at the surface in warm water, was washed ashore in considerable numbers in March 1859 at Monterey, hundreds of miles north of its usual present range. Ordinarily this species is uncommon north of central Baja California, though it penetrated into southern California in abundance in the spring and summer of 1941 (notes in California State Fisheries Laboratory).

For the region of San Francisco, in contrast, the evidence (more extensive than for the other ports) indicates a relatively stable fauna throughout the last hundred years. Approximately one hundred species have been reported as collected about San Francisco from 1853 to about 1860 (here much local collecting, particularly by W. O. Ayres, supplemented that of the Railroad Survey). With about seven exceptions, the species reported are still rather common about San Francisco. One of the seven, the opaleye, *Girella nigricans*, has not since been collected about San Francisco, but adults straggle to Monterey, and Ayres had only one example from San Francisco. Four (namely *Squatina californica*, *Rhinobatos productus*, *Synodus lucioceps* and *Stereolepis gigas*) are now very seldom found north of Point Conception, which further suggests a slight southward facies, though all of the species were reported as rare in the 1853–1860 period. Partly counterbalancing this indication of a southern facies were the early records of two northern species for San Francisco. Girard and Ayres each reported from there a snakeblenny, *Lumpenus gracilis*, which has never since been collected south of Puget Sound, and Ayres had one, the sanddigger, *Trichodon trichodon*, which has since been taken only once at San Francisco.

The relatively large number of subtropical types that were taken about San Diego and of southern California types that were secured about Monterey, from 1853 to about 1860, and the stationary habits of these species, make it appear very improbable that the northward occurrences represented merely single-season waves, such as are mentioned below. A further reason for believing that the warm-water faunas were long-lasting and real is that a considerable representation of southern types seems to have persisted through the 1870's until 1880, when Jordan and Gilbert conducted the most thorough reconnaissance of the century of the West Coast fishes. A study of the reports by Jordan and Gilbert (1881 a, b) and by their contemporaries indicates that the fauna from San Diego to San Francisco had a slightly more southern tinge than at present, despite the fact that 1880 was an unusually cold year (Figs. 1–3, 5). No particularly northern type was reported for 1880, except possibly a cod, *Theragra chalcogramma* (recorded as rarely taken about San Francisco), but in contrast a considerable number of distinctively southern types were reported for that year. A Spanish mackerel, *Scomberomorus concolor*, occurred in some numbers in Monterey Bay then and during the following several years, but it is now excessively rare even in southern California. *Cynoscion parvipinnis* was common in southern California, where it now seems to have been absent for many years, though it remains abundant in central Baja California. The barracuda, *Sphyraena argentea*, was said to be especially abundant in Monterey Bay, whereas now it lives chiefly in southern California and southward.

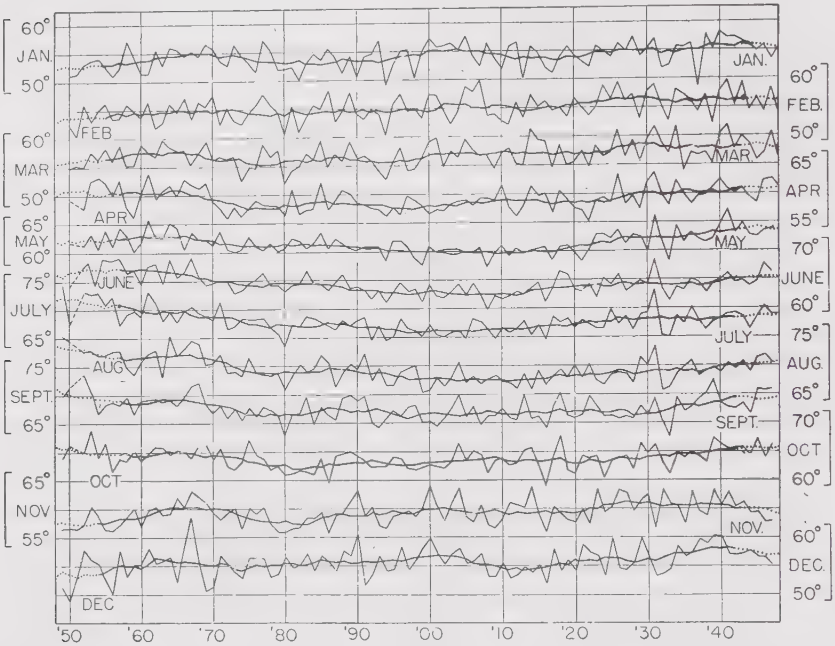

Figure 1. Fluctuations of mean air temperatures at San Diego from 1849–50 to 1947–48, for each month, with trends computed by running averages of 11. Data from World Weather Records (Smithson. misc. Coll., *79*, 1927: 934–935; *90*, 1934: 347; *105*, 1947: 373) and from Climatological Data (U. S. Weath. Bur., vols. 45–52, 1941–1948); all data corrected to means of 24 hours.

The bonito, *Sarda lineolata*, now chiefly southern, was reported to be very abundant everywhere in summer. The elasmobranch fauna as reported seems distinctly more southern than at present.

Several tropical types reported as occurring rarely in southern California in the last third of the nineteenth century possibly also represent holdovers from the warm-water fauna of the middle of the last century. Among these are three that have not since been taken in the state: *Eucinostomus argenteus, Chilomycterus affinis* and *Diodon hystrix.*

During the last two decades a considerable number of tropical types have been collected in southern California, suggesting the possibility that a slightly more tropical assemblage is becoming re-established. However, the captures are attributable, in part at least, to more thorough collecting, to chance migrations, and to the single-season northward dispersals that are discussed in the following section. Four bottom fishes previously unknown north of central Baja California, however, have been found recently in some numbers in San Diego County, with indications of recent establishment. These are the zebraperch, *Hermosilla azurea*, a porgy, *Calamus brachysomus*, and two giant groupers, *Mycteroperca xenarcha* and *M. jordani.*

SINGLE-SEASON NORTHWARD DISPERSALS OF FISH FAUNA

During occasional warm years, unusual numbers of free-swimming fishes and other pelagic animals appear along the Pacific Coast far north of their customary range. A year particularly noted for this phenomenon was 1926 (Hubbs and Schultz, 1929). Southern types, including the siphonophore *Velella*, abounded as far north as British Columbia. *Mola mola* appeared off the British Columbia and Washington coasts. Anchovies, *Engraulis m. mordax*, were unexpectedly abundant in the mouth of the Columbia River. Albacore, *Germo alalunga*, were caught near the Oregon shore for the first time on record and the catch off central California increased sharply. Mackerel, *Pneumatophorus japonicus diego*, and jacksmelt, *Atherinopsis californiensis*, previously unrecognized there, appeared in numbers in Coos Bay. A thresher, *Alopias vulpinus*, was also taken there, as a novelty, and many hammerheads (*Sphyrna* sp.) were caught in southern California.

Five years later, in 1931, an unusual number of southern fish strays were captured along the coast of southern California (Walford, 1931). In 1941 red crabs, *Pleuroncodes planiceps*, abounded off Los Coronados and Santa Catalina islands, far north of their usual range. In British

Columbia there was an intrusion of southern forms, as also in 1936 (John L. Hart, personal communication).

Similar reports stem from off the Oregon, Washington and British Columbia coasts for the summer of 1947, when July was exceptionally clear and warm. According to fishing reports, swordfish and even flyingfish appeared for the first time off Oregon, along with an especial abundance of albacore and numbers of bluefin tuna. A "yellowtail," presumably *Seriola dorsalis*, was caught off southern Washington, far north of the previously known northern limit of range. California pompano, *Palometa simillima*, appeared in unprecedented abundance in British Columbia (Hart, in press).

The appearance of southern fish on the Pacific Coast far to the north of their usual range, during warm years, has usually been attributed to the northward dispersal of individuals. Movement of this sort may be involved, at least for such fish as the sardine, *Sardinops caerulea*, and the mackerel, *Pneumatophorus japonicus diego*, that are known to migrate regularly up and down the coast. An alternative explanation, for animals with a very short life cycle, is that local populations in the north, too small to be conspicuous, may suddenly erupt when temperatures rise. More commonly, however, it is probable that the warm-water types merely move closer to shore from the warmer waters that lie outside the coastal zone of upwelling. Thus the albacore that occasionally appear close to the Oregon and Washington coast probably come chiefly from the population of the offshore, warm "blue water," rather than from southern coastal waters. This is even more likely true of *Mola* and *Velella*. The dispersal may be essentially short and transverse, like the seasonal migration of many western birds which, instead of undertaking long north and south movements, merely fly back and forth between mountains and valleys.

Whatever the course of movement may be, there is little doubt that in years when the surface temperatures are high, particularly during the spring and summer months, southern types of animals occur near the Pacific Coast far north of their usual limit of range. However, there is no regular northward dispersal comparable to that effected along the Atlantic Coast by the Gulf Stream.

TEMPERATURE DATA BEARING ON CHANGES IN FISH FAUNA

Water temperatures are available for correlation with some of these short-period shifts in fish fauna along the Pacific Coast but are inadequate to explain unequivocally any of the long-term changes. Air-temperature data, within limits, can be used as a substitute for lacking or inadequate water-temperature data, or can be used to corroborate limited data on sea temperatures, not only for current and recent years but also for the latter half of the nineteenth century. Estimates of prehistoric changes in the ocean temperatures rest on our knowledge of the temperatures of waters now inhabited by the same or similar faunal assemblages and will probably continue to rest on that basis, though some corroboration may be expected from intensive study of middens and fossil deposits and eventually from correlations of the sea-levels and associated deposits with Pleistocene history.

The noteworthy northward displacement of the marine fauna in 1926 was clearly due to exceptionally high sea temperatures along the whole length of temperate North America during the first half of that year. Hubbs and Schultz (1929) reached this conclusion from an analysis of sea temperatures at Pacific Grove, California, and of air temperatures at coastwise stations in Oregon and Washington. Sea

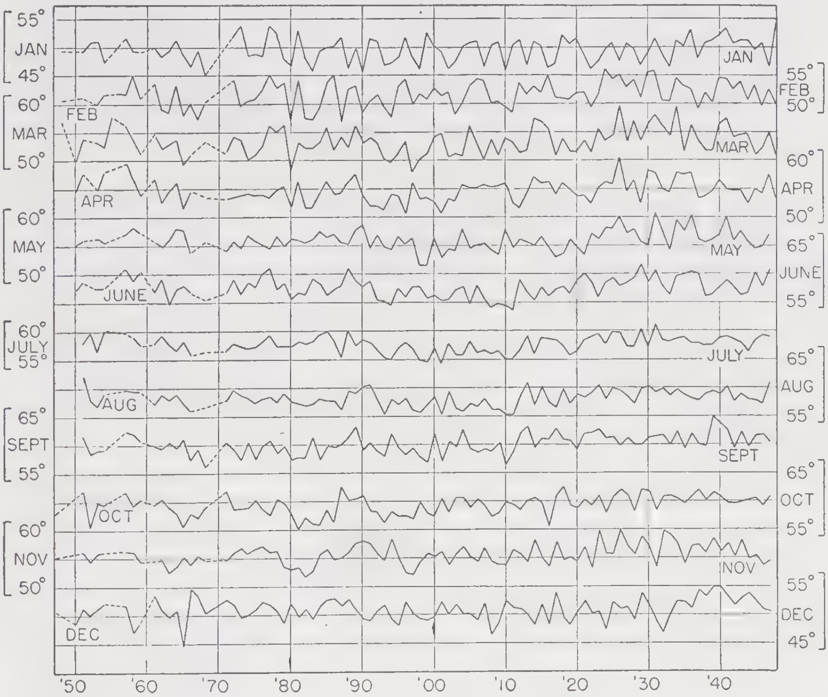

Figure 2. Fluctuations of mean air temperatures at San Francisco from 1847 (in part) to 1947–48, for each month. Data from World Weather Records (Smithson. misc. Coll., *79*, 1927: 939–940; *90*, 1934: 348; *105*, 1947: 374) and from Climatological Data (U. S. Weath. Bur., vols. 45–52, 1941–1948); all data corrected to means of 24 hours.

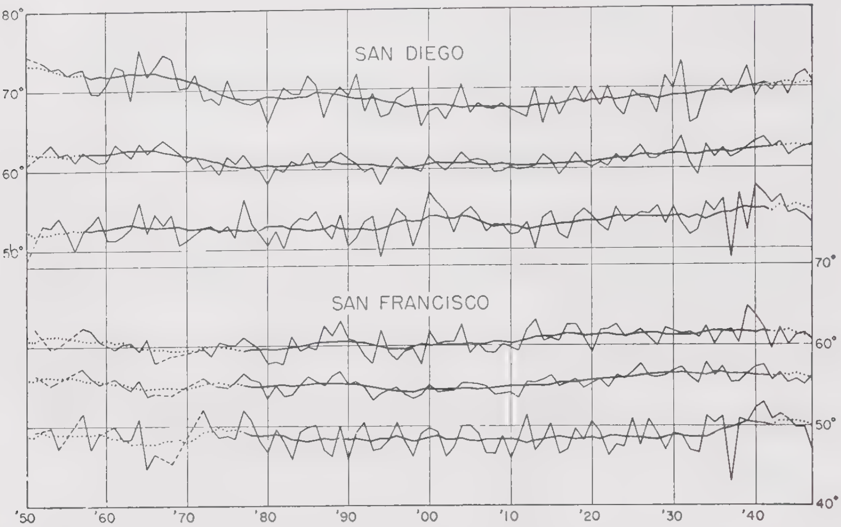

Figure 3. Fluctuations of mean temperatures at San Diego and at San Francisco, with trends computed by running averages of 11. Shown for each city are the means for the warmest month of each given year; the means for the year; the means for the coolest month. Source of data as for Figs. 1 and 2.

temperatures were high during the first half of 1926 at other stations in California (in general the correlation between stations is very close). Thus, at San Diego, the annual mean was unusually high in 1926 (Figs. 3, 5) as a result of extremely warm water during the early months of the year (Fig. 4). A similar pattern was displayed by the air temperatures at San Diego (Figs. 1, 3–5) and at San Francisco (Figs. 2, 3). At Victoria, British Columbia, the air temperatures were at or near record height from January through June and in November; about median in the other months.

During most of 1931, when many tropical fishes appeared off San Pedro, California, as well as during the latter part of 1930, the air temperatures were definitely above normal at Los Angeles and at San Diego (Walford, 1931). Sea temperatures at La Jolla (Fig. 4), closely corresponding with the air records for San Diego (Figs. 1, 3–5), were likewise extremely high from January through September 1931. The temperature increase in 1931 was less widespread than in 1926 and no record seems to have been made of any general appearance of southern forms in 1931 at any point in California north of the southern part of the state. At San Francisco the air temperatures ran about normal in most months (Figs. 2, 3). In British Columbia, however, air and sea temperatures were above normal and there was an intrusion of southern forms (John L. Hart, personal communication).

During the early months of 1941 the air temperatures were again very high (Fig. 1) at San Diego and the mean air temperature there,

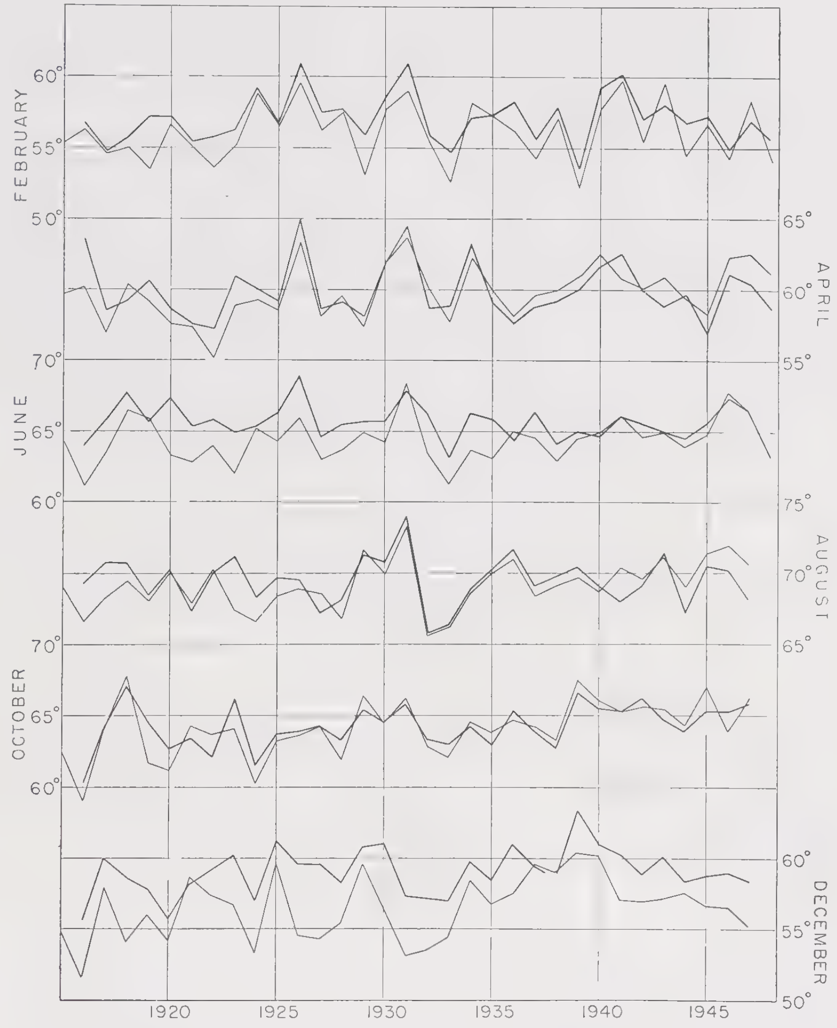

Figure 4. Fluctuations of mean temperatures for alternate months. Lighter lines represent air temperatures at San Diego from 1915 to 1947–48 (source of data same as for Figs 1–3); darker lines represent the monthly means of the sea-surface temperatures taken at 7:00 A.M. each day at the end of Scripps Pier, La Jolla.

as well as the mean sea temperature at La Jolla, was very high (Fig. 5). This is the year when the warm-water red crab, *Pleuroncodes planiceps*, abounded during the spring and summer off southern California (p. 467).

Data collected by John L. Hart of the Fisheries Research Board of Canada, from the albacore fishing grounds of the northwest coast and from the Nootka, British Columbia, lighthouse, confirm fishermen's reports of unusually high summer temperatures in 1947, when southern forms were common in the north.

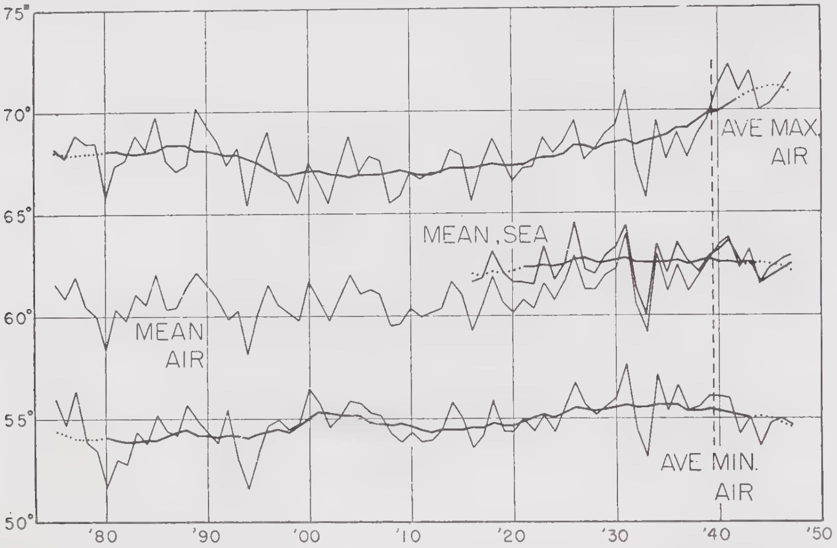

Figure 5. Comparison of fluctuations of minimum, mean and maximum air temperatures at San Diego from 1875 through 1947 with trend of sea temperatures at Scripps Pier, La Jolla, from 1916 through 1947. Annual means are plotted, with trends computed by running averages of 11 (the trend for the mean air temperature is omitted, but is graphed on Fig. 3). The upper and lower curves represent the annual averages of the daily maximum and the daily minimum air temperatures. The mean air temperatures are corrected to means of 24 hours. The vertical dashed line represents the time when the weather station was moved to a location with higher maximum and slightly lower minimum temperatures.

Greater complexities and uncertainties are involved in the effort to correlate long-term changes in the fish fauna with changes in the ocean temperatures. Air temperature data from the weather records (Figs. 1–5) stand in striking agreement with the limited though impressive data on fish faunal changes. Air and sea temperatures along the Pacific Coast are very closely correlated, as is generally known and confirmed by the data presented below, but doubts as yet unresolved pertain to the correlation of air temperature records of the last century with contemporary changes in sea temperatures.

The air-temperature data for San Diego (Figs. 1, 3–5) strongly suggest long-term climatic changes that correlate nicely with the observed faunal changes. The mean temperature seems to have been high during the early years of record, beginning in 1849–50 and continuing through the 1850 and most of the 1860 decades; that is, during the period when the fish faunas at San Diego and at Monterey were distinctly more southern than during any of the subsequent decades. From just before 1870 the general indicated trend was toward cooler weather until about 1910, after which there seems to have been a moderate reversion toward warmer conditions. In possible correlation, there is evidence—rather slight to be sure—that some subtropical fishes are becoming established in the San Diego area.

Considering the data by months (Fig. 1) we find that the changes in the trend for the mean annual temperature at San Diego characterize also the trend for each month from April through October. For two

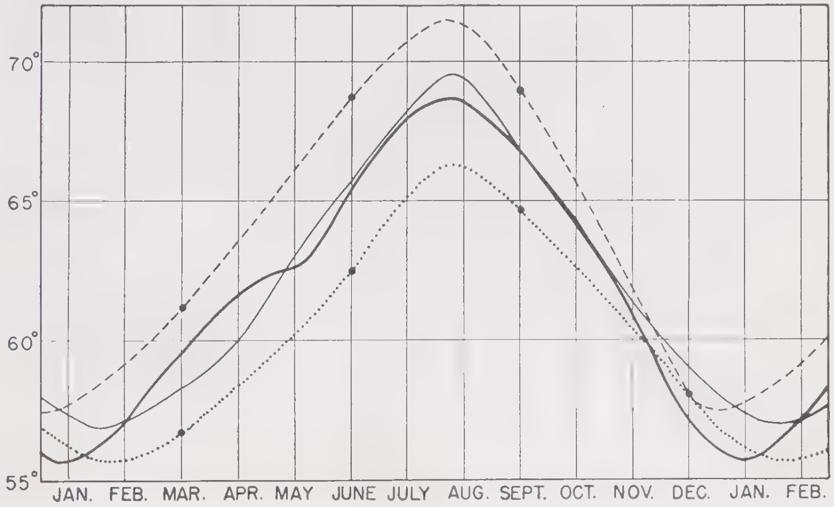

Figure 6. Variation through the year of the average sea-surface temperature about San Diego. The lighter solid line represents the trend at Scripps Pier, La Jolla, from 1916 through 1947. The heavier solid line shows the data for San Diego Bay entrance from 1854 to 1860 (probably depressed during late spring and summer for reasons given in the text). The dotted line indicates roughly the temperature cycle at present to the south of the bay entrance, computed from observed quarterly differences from the Scripps Pier data for the same year (1946–47). The dashed line is a maximum inference of the sea-surface temperatures at La Jolla, based on the assumption that the bay-entrance water came from the southward in 1854–1860, rather than from off Pt. Loma as it apparently does at present.

reasons this evidence is of particular importance in the present connection. In the first place, the months from April to October comprise the period of rapidly increasing and high sea temperatures in southern California (Fig. 6), that is, the season when the warmer-water forms of life reproduce and pass through critical stages of development. In the second place—a point that Martin W. Johnson has suggested—the indicated period of increased warmth was long enough to be of real biological significance. The fact that the months from November through March were not warmer from 1850 to 1870 than during subsequent decades, perhaps even cooler, might not have affected the northward displacement of the fauna nearly a century ago, because the region from which the southern forms would have been derived—southern Baja California—is characterized by cool winter sea temperatures as well as by warm summer seas; the subtropical forms occurring there must be adapted to cool winters.

At San Francisco (Figs. 1, 3), where there seems to have been only a slight change in the fish fauna over the last century, the air temperature data since about 1850 do not indicate a marked long-term trend downward from the 1850–1870 decades to about 1910. There seems to have been a slight downward trend, with notable irregularities, in the months from April through August.

That the air and sea temperatures along the Pacific Coast are correlated very closely is well known from the work of George F. McEwen and others and is strongly confirmed by recent analyses. There are some irregularities, for example, when offshore winds from the desert (Santa Anas) markedly raise the air temperatures but cause upwelling of cool water. Comparing the mean monthly air temperatures at San Diego with the mean monthly morning (7:00 A. M.) sea temperatures at the Scripps Institution Pier (Fig. 4, showing the data for alternate months), we find a very close agreement for the period from 1916 to 1947–48. Major discrepancies occur in certain months, notably January, June and December, but in other months the fluctuations in air and sea temperatures correspond remarkably well. For periods of several years the means and the changes from year to year may be almost identical. The curves for the annual means from 1916 through 1947 (Fig. 5) parallel one another with great precision. The mean sea temperature averaged 0.64° C. higher than the mean air temperature from 1916 through 1939 and 0.10° lower from 1940 through 1947, during which period the air temperatures were taken at a new, warmer location, as explained below.

The correlation coefficient (*c*) between the average air and sea temperatures is very high. Between the mean annual sea temperatures at La Jolla and the mean annual daily minimum air temperatures at San

Diego, for the period from 1916 through 1946, $c = 0.87$ (the minimum temperatures were only slightly reduced by the move of the Weather Bureau station). There was a similar high correlation between the mean sea temperatures and the annual average of the daily maximum temperatures: $c = 0.87$ for the period from 1916 through 1939 and $c = 0.86$ for the period from 1940 through 1946. For five years, from 1940 to 1944, the correlation coefficient between the monthly average daily sea temperatures at La Jolla and the monthly average of the daily evening radiosound surface air temperatures (approximately 2° F. higher than the minimum air temperature) at San Diego reached the astonishingly high value of 0.98. These data were computed by Dale F. Leipper of the Scripps Institution and were kindly made available by him.

Since the air and sea temperatures are so very closely correlated about San Diego, one might assume that the high air temperature records for the 1850 and 1860 decades and the low air temperature from about 1870 to about 1910, with a slight increase since, might be taken as a clear index of changing sea temperatures. Possible errors, however, are involved. From July 1849 through September 1871, the records were kept by the Army Medical Corps at various locations, by methods and with instruments that are not recorded in detail (Carpenter, 1913: Chap. I). The exact location of the station was changed several times, but fortunately the station remained at about the same elevation and within a one-half mile radius, from 1860 (about the middle of the indicated warm period) through January 1940 (Carpenter, 1913, and Dean Blake, personal communication). Thus the warm summers, the cool winters and the wide difference between the warmest and coolest months, indicated for the early years of the San Diego records (Fig. 1), can hardly be attributed to a change in the location of the station. It is suspicious that the temperature records were generally high until taken by the standard methods of the Weather Service (first under the Army Signal Service), beginning October 1, 1871. Bespeaking the significance of the indications of a prolonged warm period from 1849 through 1868, however, are the facts (1) that moderate temperatures were reported in 1869 and 1870, before the Weather Service took charge, and (2) that, with fluctuations, the trend continued downward after the methods were standardized. Considering also the striking agreement between the recorded weather data and the indicated change in fish fauna, I regard the balance of evidence as favoring the view that the trend of both air and sea temperature was downward from about 1870 to about 1910.

However, some actual data on water temperatures from 1854 to 1860 do not yield unequivocable support for the view that the sea temperatures of the southern California coast were higher then than at present (Fig. 6). These data were taken at noon almost every day from May 26, 1854, through October 31, 1860, by Andrew Cassidy, Collector of Customs and operator of the tide-gauge station that was established by the United States Pacific Railroad Survey. They are part of a set of meteorological observations made at the tide station in the entrance to San Diego Bay. The location was on the Point Loma shore north of Ballast Point, at the site long occupied by the Quarantine Station and now serving as the dock area of the Navy Electronics Laboratory (and of Scripps Institution of Oceanography). These observations, in a set of notebooks on file in the Junipero Serra Museum (of the San Diego Historical Society), were made available by Director John Davidson.

The annual mean of these temperatures taken at the San Diego Bay entrance from 1854 to 1860 are almost identical with the annual mean of the readings taken at 7:00 A. M. every morning from 1916 through 1947 at the Scripps Pier: 16.83° C. (62.30° F.) versus 16.98° C. The monthly means for 1854-60 fluctuate about the means for 1916–47: they were nearly 2° F. cooler in December and January (in correspondence with the cooler air records for these months during the same period) and nearly 1° F. cooler in August. In the probably critical spring months of March and April the means for the early years were 1.18° and 1.75° F. higher than for recent years. Though the data covered only six years, it seems probable that the winter sea temperatures of nearly a century ago were cooler, the early spring temperatures warmer, than in recent years.

It is assumed that the 1854–60 data represent ocean rather than bay conditions and that the water movement in the bay entrance was back and forth from some point near the harbor entrance. If bay conditions had ruled, the temperatures would have fluctuated widely with the tides, so that the noon readings would have varied with the progression of the tides. No such variation is apparent. In fact the readings are remarkably constant. The fluctuations within one month varied from 1° to 9° F., with an average of only 4.5° F. for the 77 months involved.

On their face value the 1854–60 data indicate, however, that the late spring, summer and fall sea temperatures were about the same as, or a little cooler than, at present, but there are reasons for thinking that the two sets of data are not comparable and that the ocean temperatures were warmer in 1854–60 throughout the spring and summer than they are now. To be sure, duplicate temperatures taken at the same spot in July and August, 1948, average about the same as the Scripps Pier records, in fact slightly higher, but the hydrographic conditions were greatly altered by the dredging of the bay and by the construction of the jetty on Zuñiga Shoal (between 1893 and 1904, according to Hertlein and Grant, 1944: 26). These actions resulted in the widening, deepening and straightening of the harbor entrance. In July and August 1948 the water surging back and forth through the entrance appeared to stem from the water near the tip of Point Loma where the along-shore water temperatures closely approximate those that extend north past the Scripps Pier (about 12 land miles due north of the harbor entrance) to the headlands near Laguna Beach. In September 1948 the bay-entrance temperatures averaged about 0.5° C. lower than those at La Jolla.

From just east and south of the harbor-entrance jetty definitely cooler temperatures prevail along shore, for more than two hundred miles (except in Todos Santos and San Quintin bays). The average surf temperatures at five "stations from the Mexican border northward to 1st and Coronado are always colder than the station at Scripps Pier. They are colder by average amounts of 1.2°, 0.5°, 0.9°, and 1.8° (C.) in the quarters beginning August, November, February and May respectively." (Dale F. Leipper, MS., based on 42, 33, 28 and 27 observations by Francis P. Shepard and associates.) Two distinct hydrographic areas are involved, with a rather sharp boundary approximately at the harbor entrance. Even slight changes might be expected to shift this boundary.

Under the conditions that existed from 1850 to 1870, when the temperatures seem to have been warmer, the cooler water to the southward probably extended to the harbor mouth and into the entrance at least as far as the point where the temperatures were taken. Changes since induced by man, particularly by the construction of a jetty, seem to confine the cooler waters so that they often do not penetrate the harbor entrance. In 1859, according to the chart of San Diego Bay, California made "From a Trigonometrical Survey under the direction of A. D. Bache Superintendent of the Survey of the Coast of the United States" (consulted in the Junipero Serra Museum), Zuñiga Shoal was tied to Point Loma by a bar having a depth of 21 to 22 feet at mean lower low water. A submerged spit extending from the shoal on the east side of Point Loma south of Ballast Point, in a direction somewhat east of south, and a slight eastward twist of the entrance channel inside the bar, both suggest that the flow in and out of the harbor involved the cooler water to the eastward and southward. If we make that assumption, and further assume that the temperature of that water was as much cooler than that at La Jolla (and elsewhere from off Point Loma northward) in 1854–60 as it was in 1946–47, when Shepard's observations were made, we may add the temperature differential determined by Leipper to the curve of the monthly means for 1854–60 (the heavy solid line in Fig. 6) to obtain a new curve that may well approximate the average along-shore temperatures from about 1850 to 1870 at points from Point Loma northward 50 miles or more. This curve, the dashed line in Fig. 6, may be regarded as a maximum estimate, and the true values may lie a little lower, but almost surely somewhat above the values that obtain at present from near Point Loma northward. Since various complications are involved, the preceding discussion should be regarded as leading merely to an approximate estimate.

By analogy and inference we may assume that the sea temperatures at Monterey were also high about 1850, or that the area of warm water extended close enough to Monterey to permit a spilling over of the warm-temperate fish fauna. About San Francisco, however, we must infer that no marked long-term changes in sea temperature have occurred since 1850.

The gradual upward trend of the air temperatures since about 1910, for all times of the year and for both San Diego and San Francisco (Figs. 1–3, 5), may well provide a false indication of warming sea temperatures. The trend might be taken as being in line with the "arctic amelioration of climate," but Dr. H. W. Ahlmann, the noted proponent of that concept, has indicated (personal communication) that the temperature changes may not have occurred (or may even have been reversed) in the approximate latitude of southern California. There is a small amount only of faunal evidence to favor a warming sea in this region over the last few decades. On analysis (suggested by Dale F. Leipper), it is found that the rise in mean air temperature at San Diego has been due almost entirely to a sharp rise in the daily maxima, which may be explained as due to the rapid growth of the city: taller buildings cut off the cooling sea breezes and more paving and masonry may cause a greater absorption of solar heat (Fig. 5). On the same basis we may perhaps account for the upward trend of the mean monthly and mean annual temperatures recorded for San Francisco (Figs. 2–3). When graphed by Leipper, the curves for the average daily maximum temperatures and for the population of San Diego correspond very closely in trend. The elevating effect of cities on temperature is a phenomenon recognized by meteorologists. For example, Hann (1903: 29–32; 1908: 38–39) stated that temperatures are usually increased 0.5 to 1.0° C. by cities. The sharp increase beginning with 1940 in the maximum daily temperatures at San Diego (beyond the dashed vertical line in Fig. 5) is definitely attributable to a change in the location of the weather station (p. 475). The trend of the surface sea temperature at La

Jolla has remained nearly level since the inception of the records in 1916, except for a midperiod rise due largely to the exceptionally warm years of 1926 and 1931, each of which was accompanied by a northward displacement of the coastwise fish fauna.

DISCUSSION AND SUMMARY

The general conclusion reached in this paper, that temperature plays a dominant role in the distribution of marine organisms, is in agreement with views generally held, for example by Ekman (1935) in his great monograph on the distribution of marine animals. The idea has been further stressed by a number of recent workers, including Stephenson (1941: 7) and Hutchins (1947). Organisms behave like thermometers in registering ocean temperatures. By reason of their stability they may often be of greater value in indicating average temperatures or in indicating peculiar seasonal distributions in temperature. Plants and animals are particularly valuable as indicators of local reversals in temperature changes with latitude.

The temporal fluctuations in temperature that seem to have been so frequent throughout the Quaternary have resulted in many faunal changes. Within historic time there have been some long-term as well as many single-season changes in temperature, with accompanying changes in the distribution of marine organisms. Such changes are stressed in the present paper, primarily for the fish faunas of the Pacific Coast of the United States. The 1850 and 1860 decades appear to have been in a prolonged warm period. The fish fauna at San Diego seems to have been much more nearly tropical than it now is, and the Monterey fauna seems to have comprised many elements now characteristic of southern California. The physical evidence for warmer waters is largely based on air temperature records. The strength of the faunal data involved is enhanced, when we note the fidelity with which the present fish faunas register the latitudinal variations in temperature. The northward occurrence of southern types in occasional years of high surface temperatures is particularly striking.

In correlating the changes in fish fauna with changes in the ocean temperatures I have given joint consideration to the biological and the physical data, in the belief that each may support the other. Consistency in the explanation of the natural phenomena of the sea has been my aim.

ACKNOWLEDGMENTS

For invaluable assistance in the interpretation and gathering of physical data I owe thanks to the master oceanographer, Harald U.

Sverdrup; to other colleagues at Scripps Institution of Oceanography, particularly Dale F. Leipper, George F. McEwen, Francis P. Shepard and Donald B. Sayner; to Dean Blake of the United States Weather Bureau, and to Margaret Calderwood of the Fish and Wildlife Service. Biological data and suggestions have come from E. Yale Dawson, now of the Allan Hancock Foundation of the University of Southern California; from my colleagues Martin W. Johnson and John D. Isaacs; from W. I. Follett, of the California Academy of Sciences; from George Y. Harry, Jr., and Donald L. McKernan, of the Oregon Fish Commission, and from John L. Hart, of the Pacific Biological Station, Fisheries Research Board of Canada. Historical aid has come from John Davidson, director of the Junipero Serra Museum of San Diego. Heber W. Blair has traced all the graphs for the figures. My wife, Laura C. Hubbs, has assisted in many ways.

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Contribution No. 380

SOUND AS A TOOL IN MARINE ECOLOGY, FROM DATA ON BIOLOGICAL NOISES AND THE DEEP SCATTERING LAYER[1]

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In studies of specific populations or communities of different animals, the investigator is concerned largely with relative concentrations of individuals and with their feeding and breeding behavior, migratory habits, etc., as individuals or as groups. Information on these aspects is fundamental to an analysis and understanding of the factors that operate as controls within the population.

Direct census of population density based on systematic collecting, and identification or direct visual observations of the population *in situ,* are time-honored methods in ecological studies, and these will always be an essential part of such investigation whenever possible. Much tedious labor is involved, however, and therefore any physical means that provides a short-cut to useful generalizations or serves as a guide to focus attention on significant aspects, such as relative concentrations and activities in space and time, serves a real need. The application of sound and of underwater photography are two very promising means to this end. Both are still largely in the exploratory stages. The present discussion will be concerned only with sound.

In the past few years a large amount of work has been carried on pertaining to underwater noise phenomena, and a number of reports

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[1] Most of the studies forming the basis of this report were made while the author was a member of the staff of the University of California Division of War Research at the U. S. Navy Radio and Sound Laboratory (now the U. S. Navy Electronics Laboratory) San Diego, California, under Contracts OEMsr-30 and NOBs-2074, respectively, with the Office of Scientific Research and Development (Section 6.1 NDRC) and the Bureau of Ships, Navy Department. Various members of the Listening and Echo Ranging Sections assisted in the studies, and acknowledgment is made especially to Mr. R. R. Carhart for preparation of Fig. 1, and to Mr. G. Duvall and Mr. R. L. Ely, physicists, who collaborated in study of the deep scattering layer.

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have been written relative to the behavior of sound in water, spectrum analysis, and identification of ambient noises, but it seems desirable to examine and interpret some of the information from an ecological rather than an acoustical point of view, to present new data and to point out some possible uses that suggest themselves.

There are two principal ways in which sound, depending upon its origin, may serve in biological studies: (1) Underwater sound voluntarily produced by the animals and picked up on appropriate hydrophones and analytical equipment, and (2) sound projected as signals from sonar gear, such as from ships' fathometers or echo-ranging devices, and returned as reflected sounds by organisms.

UNDERWATER SOUNDS PRODUCED BY ANIMALS

The significant sound-producing marine animals fall into three general groups: (1) Crustacea, (2) fishes, and (3) mammals. Only the first two will be considered here.

Crustacean Noises

The crustacean sounds are by far the most widespread and persistent of all known underwater biological noises. This is due to the remarkable claw-snapping habits of two genera of snapping shrimps, *Crangon* and *Synalpheus*, widely distributed in tropical and subtropical waters (Johnson, 1943a).

The characteristic continuous loud crackle caused by populations of such shrimp is readily distinguished instrumentally from other ambient noises because of its continuity and high frequency (up to 50 kc) and great sound pressure spectrum level in the neighborhood of 10 to 15 kc.

The degree to which shrimp crackle dominates the noise in shrimp habitats has been discussed elsewhere (Johnson, Everest, and Young, 1947). It is instructive to consider here mainly the operation of directional hydrophones in seeking out these habitats. Fig. 1 shows results of a survey near San Diego when equipment of the type capable of 360 degrees rotation in a horizontal plane was used. The shrimp habitat at the point where these observations were made is a ledge of shale one mile in width in water of about 10 to 20 fathoms in depth. The shale is heavily pitted by borings and crevices made largely by boring mullusks.

It is seen from Fig. 1 that at a distance of 4,000 yards from the edge of the shrimp habitat the sound spectrum level at 20 kc is low and uniform in all directions, as shown by the solid black area in the center of the circles of pressure levels. Both depth and bottom conditions here were unfavorable to snapping shrimp, and the noise recorded is

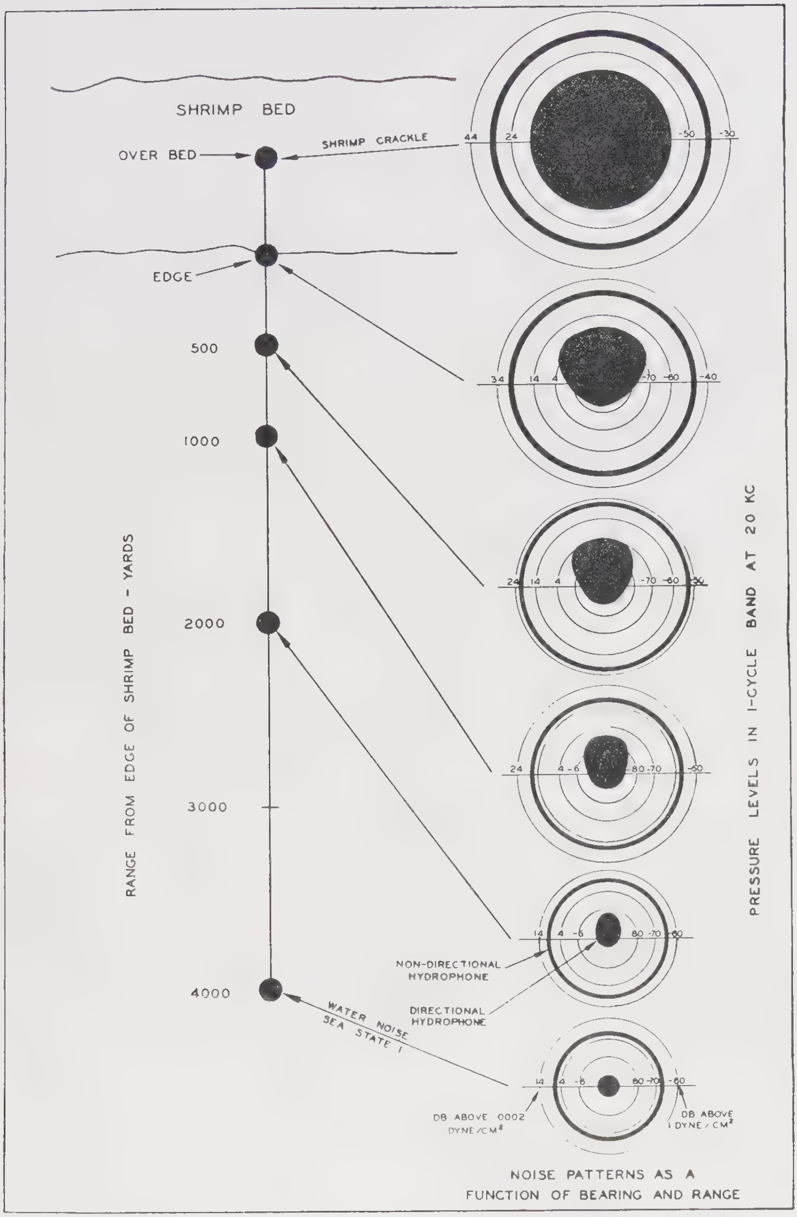
SHRIMP BED
OVER BED
SHRIMP CRACKLE
EDGE
500
1000
2000
3000
4000
RANGE FROM EDGE OF SHRIMP BED - YARDS
WATER NOISE
SEA STATE I
44
24
-50
-30
34
14
4
-70
-60
-40
24
14
4
-70
-60
-50
24
4 -6
80 -70
-60
14
4
-6
80
-70
-60
NON-DIRECTIONAL HYDROPHONE
DIRECTIONAL HYDROPHONE
14
4
-6
80
-70
-60
DB ABOVE 0002 DYNE/CM²
DB ABOVE 1 DYNE/CM²
PRESSURE LEVELS IN 1-CYCLE BAND AT 20 KC
NOISE PATTERNS AS A FUNCTION OF BEARING AND RANGE

Figure 1. Snapping-shrimp noise as detected with a directional hydrophone, with its beam rotated horizontally through 360°, over and at various distances from the shrimp bed.

"water noise." But upon approaching the ledge, there is a gradual increase of high frequency sound from the direction of the "shrimp ledge." Because of the directivity of the hydrophone, this increased sound spectrum level shows on the noise pattern as an expanding lobe in the direction of the shrimp bed. The angle of the high noise level increases as the bed is approached, indicating a habitat of great extent. When over the large shrimp bed, the sound spectrum level is again uniform in all directions, but because of intense shrimp crackle it is at a very much higher level than at 4,000 yards from the bed. Upon passing over the bed to the opposite side, where there is a shallow water area (not shown in Fig. 1) with sandy bottom, the sound spectrum level gradually diminishes and the lobe in the noise pattern again points towards the ledge, indicating that the ship now was over a habitat unfavorable to shrimp, apparently because of the sandy bottom.

The sound spectrum level obtained with the nondirectional hydrophone is shown as heavy circles in Fig. 1 for comparison.

In this manner additional information is gained besides that obtained from laborious dredging, which is often extremely difficult or impossible to accomplish. Illustrative of this are the results from dredging in an area of boulders at a depth of 10 fathoms off San Diego, where dredgings failed to yield more than an occasional shrimp, although the shrimp crackle was exceedingly loud over the area, indicating that shrimp are no doubt very abundant there (Fig. 2). Clean boulders have been brought up, but the agile shrimp appear to escape the slow moving dredge, so that their capture is only a matter of chance.

Direct and Indirect Uses of Shrimp Crackle

The crackling of shrimp may be used indirectly to some degree in the study of other benthic animals with which the shrimp are symbiotic or form more or less intimate environmental associations.

The possibility of using shrimp crackle in the study of certain large sponges, including the commercial sponge, should not be overlooked. It is well known that a number of snapping shrimp species, living within the pores and channels of sponges, can be heard when the sponge is removed from the water. A single sponge (*Spirastrella*) has yielded several hundred shrimp (Hay and Shore, 1915–1916). Though not yet demonstrated directly, there is reason to believe, on the basis of what has been said, that shrimp crackle might serve a commercial purpose in determining the location and extent of sponge concentrations.

The large amount of data showing a sharp drop in shrimp crackle at depths beginning at about 30 fathoms is convincing corroborative evi-

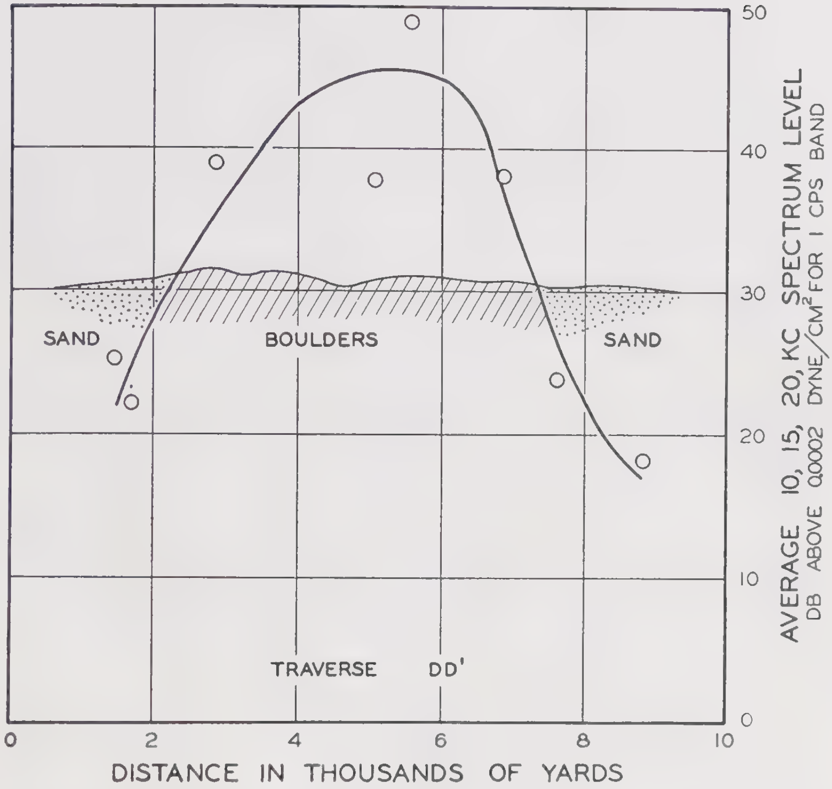

Figure 2. Sound spectrum level of shrimp crackle across a boulder patch in ten fathoms (from Johnson, Everest, and Young, 1947).

dence that this depth marks the maximum at which most species of *Crangon* and *Synalpheus* live in concentrations sufficient to provide instrumental measurements of their crackling. This is in keeping with an analysis of the vertical distribution of these genera as shown in 3,483 dredge hauls from various depths by several major expeditions, but the ease with which the information was obtained through acoustic means is in striking contrast.

The regularity with which shrimp crackle is found in, and is confined to, areas of certain bottom types, such as rock, coral, coarse shell, weed, and litter of harbors, is evidence of the importance that must be attached to the ecological factor which provides easily-maintained shelter for these animals.

If high sound level of crackle is an indication of the general type of bottom, and since other animals, including some fish, frequent (in some cases confined to) rocky or coral bottoms where snapping shrimp abound, then the noise may serve as a guide to these areas. Examples of such areas are the fishing grounds off North Carolina where isolated coral patches occur (Radcliffe, 1914). Shrimp crackle has been reported from one of these grounds by Dobrin (personal communication), and doubtless it occurs on others as well. On the California Coast, where the agariferous seaweed *Gelidium* is harvested on rocky bottoms, the divers have remarked that they can "hear the *Gelidium* crackle." Though this is an erroneous interpretation of the origin of the sound, the implication is clear.

Ecological Significance of Diurnal and Seasonal Variations in Shrimp Crackle

Certain ecological facts may be gleaned from a study of the diurnal and seasonal variations in shrimp noise.

Diurnal Variations in Activity. It is well known that many intertidal animals that can be observed during low tide, or at the water's edge, become increasingly active at night. Among these are the crabs, isopods, limpets, and other gastropod mollusks. This increased activity may be explained as an adaptation that is advantageous to the animals in avoiding daytime dessication during low tide and in avoiding the ravages of preying birds.

Is this instinctive nocturnal activity reflected equally in the animals that live in deeper water below the low tide level? A commensurate answer to this question is not readily obtained.

Acoustical measurements of shrimp crackle do, however, give evidence of a marked nighttime increase in noise. These measurements have shown a 2 to 5 db increase in sound pressure spectrum level of crackle during the night, with peak levels just after sunset and shortly before sunrise. The figures are logarithmic expressions, which, interpreted into terms of shrimp activity, reveal a two to threefold increase and perhaps reflect an over-all activity within the shrimp community. Involved in this activity are not only the shrimp but also other animals, who, by their increased wandering about, cause increased irritation to the shrimp and hence more frequent individual snapping.

Annual Variations. Studies on seasonal variations have been made only in the San Diego region where the seasonal variation in temperature is about 8° C. However, these studies do not reveal fluctuations in shrimp noise that are greater than those observed diurnally. From this it might be concluded that there is a rather uniform year-round population of adults capable of snapping, which implies that there may be a production of overlapping generations that do not migrate. In this connection it would be of interest to note what effect a greater range of temperature would have on activity in such an area as Beaufort, North Carolina, where the range is about 20° C, where snapping shrimp are abundant and where sound level due to them is known to be high during early spring and summer. A marked seasonal change in noise level might be inferred as a measure of the effect of temperature on the activity of the shrimp community.

Regarding the application of other crustacean sounds, little can be said. Several species of spiny lobsters produce a strident grating sound when they rub specialized structures on the bases of each of the antennae against opposing structures on the carapace. The sound is readily heard under water over acoustic instruments, but no attempt has been made to use it in locating populations. Indications thus far show that the sound is too rarely produced to be of general ecological use, but seasonal variations and local differences have not been sufficiently investigated.

Fish Noises

Many fishes are known to produce noises when removed from the water, but it is uncertain as to how many of these are soniferous in their natural habitat (Burkenroad, 1931). However, there are a number of notable sound-producers with organs well adapted to generation of underwater sound. Among these are especially the Sciaenidae (croakers and drums), the toadfish *Opsanus*, the singing fish *Porichthys*, and the searobin *Prionotus*. Additional underwater sound-producers are listed by Knudsen, Alford and Emling (1948), who also discuss the characteristics of fish sounds as related to "water noise." Other spectral analyses of fish noises are given by Loye and Proudfoot (1946) and Dobrin (1947).

The data available on fish sounds have not been collected or examined as closely with a view to their ecological application as was done for the shrimp studies. The most challenging suggestions come from the acoustical studies of the croaker, *Micropogon undulatus*, in Chesapeake Bay; the toadfish, *Opsanus tau*, at Beaufort, North Carolina; and various croakers at La Jolla, California.

The chorus of sounds produced by *Micropogon* in Chesapeake Bay was reported upon by Loye and Proudfoot (1946). Their findings include several items of ecological interest. (1) The chorus was heard only in the evening and nighttime. The interpretation suggested was that the noise accompanied a period of feeding. (2) The maximum nighttime intensities of the noise were localized to a specific area. (3)

Fish of this type appear to become accustomed to unusual noises, such as underwater explosions of blasting caps when these are detonated during the chorus. (4) Spectrum analyses of croaker noise in May 1942 showed appreciably more energy at frequencies up to 2,000 to 2,500 cps than three months later when there was very little above about 1,000 cps. It was suggested that the fish in the bay had grown during this period and that the correspondingly larger air bladder, which acts as a resonator, resulted in lower frequencies. However, the growth rate of sexually mature *Micropogon undulatus* is only about two to three inches in a year, according to Hildebrand and Cable (1930), so the size increase during three months could not be very great. Actually, the spectrum analysis probably revealed a means of testing a local population shift, which in this case resulted in the younger (smaller) fish being replaced in the area by an older population or by an admixture of older forms sufficient to lower the average sound frequency.

During a preliminary survey (Johnson, 1943b)[3] of underwater noise at Beaufort, North Carolina in April 1943, the most conspicuous noise encountered in Beaufort Harbor, other than shrimp crackle, was a soft cooing sound that was produced as isolated notes both day and night. This sound, later studied in detail by Dobrin (1947), was believed by him to be produced by the toadfish. The outbursts, as heard over the nondirectional hydrophone, always appeared to come from fixed locations on the bottom where they persisted for days at a time. They were found to be associated with the nest building habit of *Opsanus*. This is interesting evidence of persistent guarding of the nest or area as well as maintenance of a system of territorial rights, an instinctive habit known to be common also for some other fish.

In the summer of 1942 a chorus of fish noises was discovered at the outer end of Scripps Institution pier, which extends 1,000 feet outward from shore. Since that time, except for the spring and summer of 1946, and the summer of 1947, listening observations have been carried on at irregular intervals throughout the year. From these it was found that the chorus began in the spring about May 3, 1943; April 11, 1944; April 25, 1945; May 14, 1947. It continues throughout the summer and disappears about the middle or latter part of September. There are only occasional individual outbursts of sound at other seasons.

The chorus begins about sunset and increases gradually to a steady uproar of harsh froggy croaks, with a background of soft drumming.

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[3] Thanks are due to Dr. H. F. Prytherch, Director of the U. S. Fish and Wildlife Service Laboratory, for facilities at Beaufort.

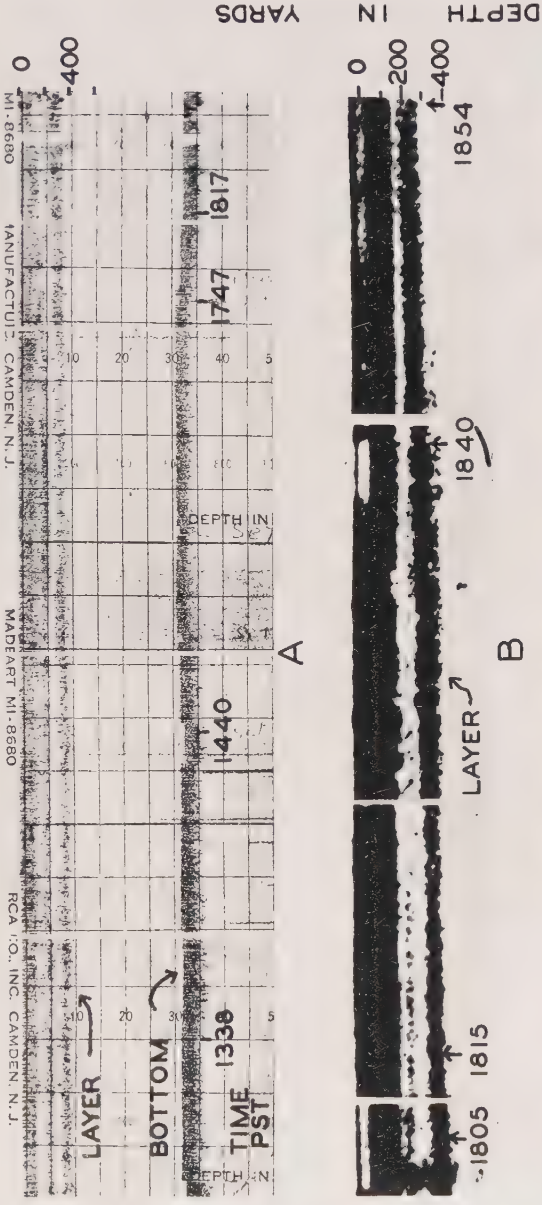

Figure 3. Fathograms of Deep Scattering Layer, 18 kc, E. W. Scripps, 1945, off San Diego: *A*, Layer during afternoon of June 26; *B*, Layer ascending August 18; *C*, Layer descending August 19.

This continues unabated for two to three hours and finally tapers off to individual outbursts at rare intervals. From tests and recordings of isolated fish in aquaria, it seems clear that the chorus consists of one or more of the following species of Sciaenidae: black croaker, *Sciaena saturna;* spotfin croaker, *Roncadro stearnsi;* yellowfin croaker, *Umbrina roncador.* Each of these fish produced vigorous froggy croaks which were nearly identical to those heard in the "chorus." In addition to croaking, *Sciaena saturna* produced a series of rapid clicking sounds. In the tests, none produced sounds similar to the soft background drumming.

Although tests of the black croaker demonstrated that individual fish are capable of producing more than one kind of sound, the soft drumming in the chorus may be produced by a species not tested, for it was never a part of the chorus during the first weeks in spring.

Further evidence which strengthens this view was obtained in July 1945 when listening alternately over stationary hydrophones, one placed at the pier and one at a distance of 2,000 feet from the pier. The sounds picked up on the distant hydrophone were dominated by the soft drumming, whereas on the nearer hydrophone the harsh croaks were dominant, with only a rare outburst of drumming. Thus it appears that two separate schools of different fish were involved.

The above is the only locality where a "croaker chorus" has been observed along the west coast, though individual outbursts are often heard elsewhere. Evening listening tests have been made at a few other locations with negative results, but it is highly probable that many other such choruses do hold forth at other localities south of Point Conception. The significance of this croaking in unison is not known, but it is difficult to believe that so marked and regular a phenomenon does not have some ecological significance.

REFLECTED SOUNDS

The Deep Scattering Layer

The "deep scattering layer" refers to a sound scattering layer within the sea. This layer, which was first observed in 1942 (C. F. Eyring, R. J. Christensen, and R. W. Raitt, 1948), may have a thickness of about 50 fathoms and be spread horizontally over vast areas at depths of 150 to 450 fathoms during the daytime. Outgoing signals of 18 kc frequencies are more or less scattered by reflections from bodies of scatterers that make up the layer. This results in more or less pronounced "false bottoms" being indicated on the recording fathometer tapes.

Biological Hypothesis

Precisely what these sound-reflecting bodies are is not known, but while working from the author's hypothesis that the deep scattering layer may be caused by stratification of either planktonic life or nektonic forms associated with the plankton, it was possible, in a 24-hour series of observations on June 26 and 27, 1945 aboard the E. W. Scripps, to show for the first time that the layer is not stationary at any depth but that it behaves biologically in performing vertical diurnal migrations in a manner paralleling the well known behavior of many planktonic animals (Anonymous, 1946).

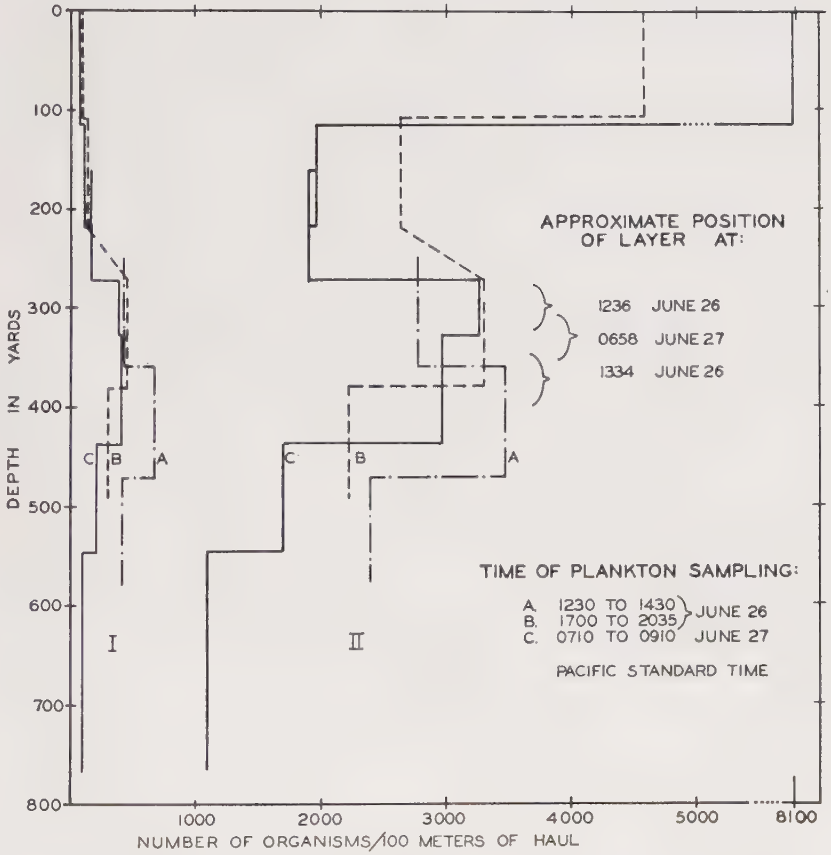

Figure 4. Vertical distribution of zooplankton. I. Animals greater than 2 mm. II. Animals 2 mm or less.

The observations were made about 20 miles off Point Loma where the depth is 660 fathoms. Fathograms were made of the layer from about noon June 26 to noon June 27 (Fig. 3). During this time it moved towards the surface in the evening and descended again the following morning, apparently under the stimulus of changing light intensity. It reached its maximum depth in early forenoon, suggesting that while light was the stimulus initiating the downward movement, some other factor (which might be temperature or pressure) became dominant in limiting the depth of descent. The partial or complete disappearance of the layer at night may result from a tendency of the scatterers to become dispersed as a result of the absence of the stimulus (light) which in the daytime causes them to accumulate in a relatively narrow zone.

Using the fathometer as a guide to the position of the scattering layer, a series of 14 vertical plankton hauls were made below, through and above the main layer (a faint secondary layer was indicated above the main layer). Nansen closing-type nets with No. OX and No. 8 bolting silk and a 40-cm mouth were used.[4]

In Fig. 4 is given the number of animals caught, adjusted to 100 meters of haul and shown as two size groups, *i. e.*, those greater than 2 mm in length and those 2 mm or less.

The daytime vertical distribution of the zooplankton was similar in general for the two days. The preponderance of smaller forms (mainly copepods 1 to 2 mm in length) in the 0 to 110 yard stratum was very striking. Below 110 yards the number of this size fell off markedly but increased again to a secondary maximum which in the early afternoon of June 26 was at about 360 to 475 yards, partly within and partly below the scattering layer. In late afternoon the maximum was somewhat higher and within the layer. On June 27, the secondary maximum of smaller forms was within and somewhat above the layer.

Animals of size greater than 2 mm in length showed a small increase within the scattering layer on both days. Most abundant of these were copepods ranging from 2 to 8 mm and including mainly *Calanus* and *Metridia*, but also *Heterorhabdus*, *Euchaeta*, *Eucalanus*, and *Rhincalanus*. The largest organisms caught were sagittae (total 35) ranging from 6 to 27 mm. Included also were a few euphausiids, ctenophores, medusae, polychaetes, and amphipods. Previous work in this area has often shown daytime swarms of euphausiids at depths below 200 yards. They are relatively strong swimmers and are capable of avoiding small nets during the daytime.

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[4] It is obvious that in order to obtain larger samples and to minimize the effect of patchiness, horizontal tows should be resorted to in sampling the various strata. But samples collected in this manner at the deeper levels have thus far appeared unreliable because of the difficulty of maintaining the net within the narrow horizontal limits required.

The largest body cross section for animals other than the medusae was only 5 mm, and none of the animals was found to have air bubbles which would make them strong scatterers (cf. Raitt, 1948). Yet from these preliminary observations there appears to be some direct correlation of the planktonic animals with the scattering layer. If the size and acoustic properties of these forms are not suitable to scatter sound, the alternate explanation must then be that larger forms not sampled by the small, slowly moving net are responsible and that they occur more or less concurrently with the small planktonts upon which many of them presumably subsist. The larger fast swimming forms must include euphausiids, prawns, deep-sea fish, and squids, for it is well known that all these do frequent the waters within the range of the scattering layer.

The fact that correlation appears to be best with the larger planktonts may be of special significance. It suggests that many of the larger scatterers are not strictly filter-feeders (that is, do not filter out the small forms less than 2 mm in length with fine gill rakers, etc.) but probably select more or less individually the larger planktonts. The feeding habits of these deep-sea forms have received little attention, but the manner of feeding can be inferred largely from study of feeding structures. Fish such as the cyclothones, myctophids, and the hatchet fish (*Argyropelecus*) are not strictly of the filter-feeding types, nor are the squids. Hersey and Moore (1948) have recently shown the deep scattering layer to be widespread in the Atlantic Ocean, and present evidence that the euphausiids are perhaps among the planktonic forms involved as scatterers.

The rate at which the layer ascends or descends may be a measure of swimming speed and therefore may be an aid in deducing what animal groups might be involved in its formation. This rate apparently varies somewhat. In the June 26–27 observations the maximum rate of ascent appeared to be around six feet per minute. The record for August 18–19, 1945 aboard the E. W. SCRIPPS in the same area (Fig. 4 B and C) gives approximately the same rate of movement. According to the clearest records obtained by Dietz (1948) in an extensive survey of the geographic range of the layer, the rate of movement is 10 to 18 feet per minute. This rate of movement would exclude many slow swimming planktonic forms. However, the adult stages of such planktonic animals as euphausiids, chaetognaths, and amphipods can easily swim at this speed, and when under a directive stimulus, such as decreasing or increasing light, they might be expected to migrate vertically at a speed paralleling that observed in movements of the layer. Preliminary tests show that, for short distances at least, euphausiids are capable of swimming at rates ranging upward to 39 feet per minute, and the copepod *Eucalanus* as high as 30 feet per minute. The deep-sea fishes, such as the myctophids, sometimes caught in deep plankton hauls in this area, do not possess air bladders which would limit the speed of their vertical movements because of change in the hydrostatic pressure. At night they are also commonly caught at the immediate surface.

The vast extent of the layer (sometimes present for a whole day's run of the ship) presupposes an abundant and rather uniformly scattered community that shows up on the fathogram as being more widespread than schools of fish or squid commonly observed near the surface. Squid have been suggested as the probable cause of scattering (Lyman, 1948), but while they may be expected to be a part of the scattering layer along with other animals, the type of squid known to be abundant, i. e., *Loligo*, has been observed to school at the surface. If this habit is not abandoned when they are present at great depths, then it might be expected that they would appear as limited patches on the fathograms. For example, Tester (1943), in a study of reflected sounds applied to fisheries, has shown how schools of herring in shallow water can be detected as patches on the fathograms.

The acoustical evidence does not readily lead to the assumption that only one kind of animal is involved. On the other hand, Russell (1928) has reported a different migratory response for different age groups and sexes of copepods.

The daytime formation of two scattering layers, or the splitting of the layer, with one part migrating upward with increased darkness while the other remains stationary, as shown by Dietz (1948), presents complicated and intriguing problems for the ecologist. Do the layers represent segregations of different species, stages of development, or sexes?

These are questions that remain to be answered, but with the aid of acoustic gear as a guide to collecting the solution should be greatly simplified.

SUMMARY

Underwater sounds produced by animals or reflected by them can be used in studying concentrations and behavior of certain marine populations.

Biological Sounds. Crustacea and fishes are the main sound producers. Crustacean sounds consist mainly of high frequency crackle produced by snapping shrimp. With directional sound equipment,

their habitats can be detected to distances of 2,000 yards or more.

Studies of the continuity and sound spectrum level of shrimp may give evidence pertaining to stability of populations, their diurnal activities, geographical distribution, and type of bottom and depth of water preferred.

Observations on fish noises have given less useful ecological data. They do, however, demonstrate a regular and pronounced seasonal and diurnal habit of certain Sciaenidae to form localized choruses, as contrasted with isolated solos by the toadfish (*Opsanus tau*).

Reflected Sounds. The "deep scattering layer" has been shown by its diurnal vertical migrations to be biological in nature. The partial reflection of fathometer signals in this layer promises to be a useful ecological tool in studying the organisms involved.

While using sound as a guide, a preliminary study in 1945 showed a positive correlation with plankton stratification and the depth of the scattering layer. This relationship may be partly secondary, since the more effective scatterers may be larger forms that subsist upon and migrate more or less concurrently with the plankton.

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Contribution No. 381

FOG DEVELOPMENT AT SAN DIEGO, CALIFORNIA

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INTRODUCTION

If true fog alone be considered—that is, suspended water particles which reduce horizontal visibility at the earth's surface to 1,000 meters (or ½ mile) or less—then fog at San Diego occurs nearly four times as frequently during the winter period, from October through April, as during the remaining months of the year (11, p. 34). Yet, of the many studies of California fog which have been made, none appears to be concerned directly with coastal fog in the winter period.

The fog situations during several winter periods were examined at Scripps Institution. Particular attention was paid to air mass characteristics at various altitudes relative to sea surface temperature. It became apparent that nearly all of the fog situations developed in a systematic manner over a period of days, and that the developments resulted from the effect of local influences upon a given set of initial conditions. The purpose of the following discussion is to describe this development, to present a model, and to give statistical evidence showing the pertinence of the concepts involved.

A MODEL DEVELOPMENT

A model has been devised to illustrate the manner in which fog situations develop in the San Diego area. The model is described in four different stages beginning with the initial conditions which are required if the development is to take place.

The dominant feature of the initial conditions is the presence over the sea of air which has a temperature higher than the sea surface temperature and which is relatively dry aloft. The high temperature of the air guarantees that an inversion will be formed at the surface to restrict the vertical movement of moisture and thus cause a thin lower layer of air to approach saturation. The dry air aloft permits

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rapid cooling of the surface layer and intensification of fog by radiation.

The initial conditions for fog formation may be brought about when the Pacific anticyclone pushes inland over northern California and causes a general easterly flow, so that the air arriving at San Diego has moved down the slope of 4,000-foot mountains. Air following such a path is necessarily warm and dry at San Diego. Out of 42 winter fogs occurring in 1943 to 1945, 39 were preceded or accompanied by easterly winds aloft. The typical synoptic weather situation is shown in Fig. 1.

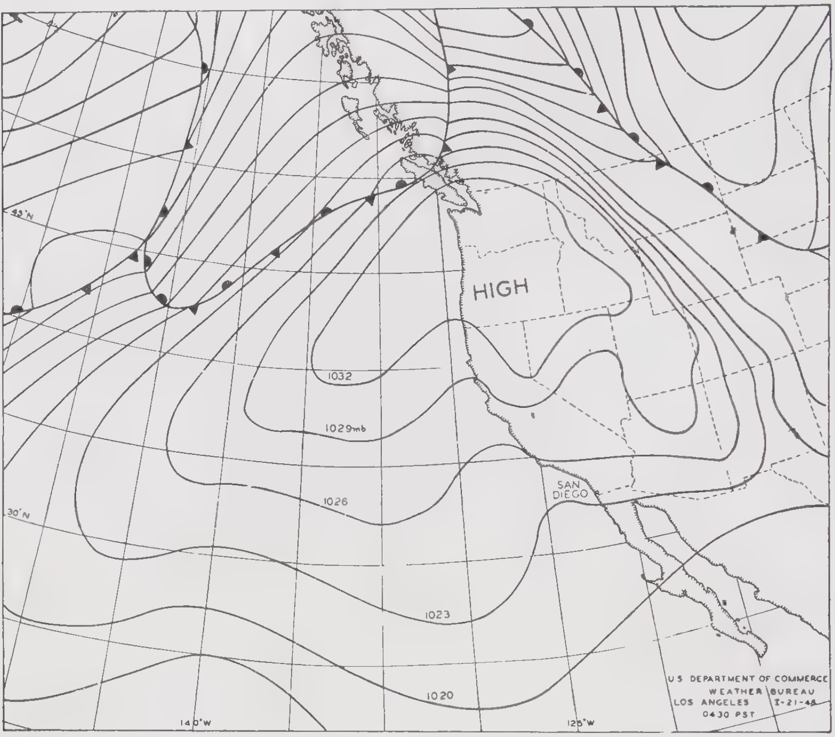
45°N
HIGH
1032
1029mb
1026
30°N
SAN DIEGO
1023
1020
140°W
120°W
U S DEPARTMENT OF COMMERCE
WEATHER BUREAU
LOS ANGELES 1-21-48
0430 PST

Figure 1. Weather map showing the type of synoptic situation which usually precedes winter fog at San Diego.

In the second stage of the fog development, the easterly air flow weakens as the high-pressure cell is divided into two parts, one on each side of the coastal mountains. Flow of warm dry subsiding air toward the sea decreases, and the locations of the high-pressure cells permit the air offshore from San Diego to remain in a relatively stagnant condition. The moisture content of the lower layers increases due to evaporation from the sea, and the heat content of these layers decreases due to conduction of heat downward (9). A surface inversion is formed, and the lowest air layers become nearly saturated at a temperature close to that of the underlying sea surface.

In the third stage, the normal northwesterly airflow and seabreeze regime returns and fog forms. The details of formation cannot be described as yet, but observations indicate that formation occurs over regions of low sea surface temperature. Fig. 2 shows a tongue of relatively cold water which is consistently found in the same area. Fog formation is often observed here (1). Also, fog is often found along the coastline where observations during eight winter cruises by the buoy boat of the Scripps Institution have shown a band of water which is at times several degrees colder than the sea surface ten to

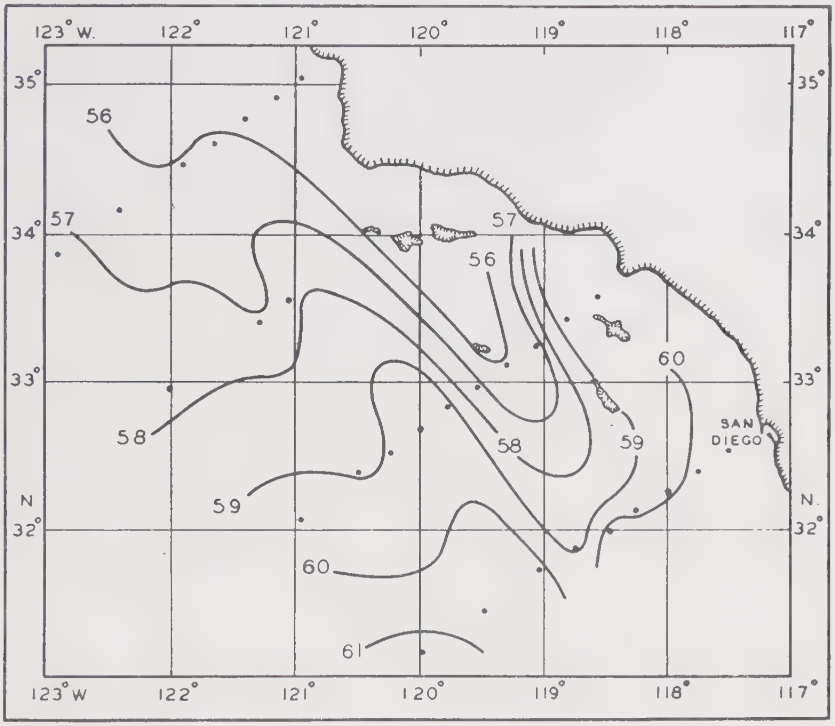

Figure 2. Sea surface isotherms in degrees Fahrenheit based upon a cruise of the E. W. Scripps, February 15 to 25, 1938. Observations were made where dots appear.

fifteen miles offshore. In the situation shown in Fig. 2, the average sea surface temperature at Scripps pier near San Diego was 14.3C (57.8 F) and that offshore was 15.6C (60.0 F).

Changes in humidity and heat content which occur during flow of nearly saturated air across sea surface isotherms may cause the formation of fog. If these changes do not form fog, they appear to bring the thin lower layer of air into such a state that large amounts of heat are lost by radiation from the moist air, and fog is formed by this means (4).

Once fog is formed, radiation from the cloud cools the thin, nearly stagnant fog layer to a temperature several degrees lower than the sea surface temperature. Under these conditions there is continual upward flux of heat at the sea surface, but the air remains colder than the sea. The lapse rate of temperature is nearly dry adiabatic (7). Since the air is colder than the sea, evaporation continues even though the water vapor is saturated (9). Thus, radiational cooling causes first a decrease in temperature and then an increase in evaporation. Both of these effects markedly intensify fog and serve to maintain it.

As the sea breeze strengthens during the daytime, the fog is carried shoreward and is likely to arrive at the coast in the late morning or early afternoon. The day on which it will first arrive is determined by the time at which the pressure gradient, which caused the initial easterly flow, weakens sufficiently to permit a sea breeze to develop.

When the fog layer first arrives at the coast it is usually quite thin and is soon dissipated by the daytime heat of the land; thus the fog does not extend inland. Since the temperature at the surface increases rapidly as the air moves inland, the moisture is carried upward and the dew point inland from the coast does not increase materially. At night, the sea breeze weakens, and moisture is no longer brought toward land. Thus, there is not sufficient moisture for fog to be formed inland either during the day or during the night.

Stage four of the fog development occurs when the nearly adiabatic layer deepens to approximately 400 feet or more. The increasing westerly winds and sea breezes and the convection resulting from radiational cooling at the cloud top contribute to this deepening. Evaporation from the sea continues and the presence of the strong inversion still restricts the vertical movement of moisture, thus maintaining a high dew point in the marine layer (the nearly adiabatic moist layer). Fog is present over the sea both day and night. During the day the sea breeze carries the fog toward shore. The daytime radiation and conduction of heat from the land mass dissipate the fog as it approaches shore, but the nearly adiabatic layer, being deeper than in the previous stage, is not destroyed as rapidly. It retains its high moisture content in the form of vapor and moves inland. At night, the air over the land cools and fog is formed in the moist layer. As cooling continues, this fog may spread and join with the fog offshore.

As the marine layer below the inversion continues to deepen, the point is reached where the mixing and cooling processes do not result in condensation throughout the entire layer. The upper portion is filled with water particles first and fog does not form on the ground. Thus, the fog sequence is ended and the stratus regime begins. The complete fog sequence usually extends over a period of about five days.

In the actual development of a particular situation, deviations from the above transformation may be observed. For example, on rare occasions the entire sequence may take place in a period as short as one day; a normal sequence may be interrupted or terminated at any stage by the passage of a front or an upper pressure trough; or, after the easterly winds have weakened and fog development has started, the winds may strengthen again, thus temporarily reversing the development. In spite of the deviations of particular cases from the model, nearly every case of fog in the winter period may be identified with the development described above.

AN OBSERVED DEVELOPMENT

In Fig. 3 are shown the soundings for seven successive days in January 1948. Sounding A shows the presence of dry air warmer than the sea to heights as great as 2,000 feet, which indicates the existence of stage one described in the model development. This is a warning of fog to come. The synoptic situation associated with the influx of this air is similar to that of Fig. 1, the time of the map being nine and one-half hours after the time of the sounding. Sounding A is an afternoon sounding which was used because the morning observation was not available on this day. The remainder of the soundings in Fig. 3 are early morning observations made at 24-hour intervals.

Sounding B shows that a surface inversion has formed and that the surface air temperature is lower than the sea surface temperature. This indicates that stage two occurred between soundings and that stage three exists. Fog arrived at the coastline at 1710 PST (Standard Time at 120° W) on the afternoon following the sounding, January 21. The air temperature in the fog as it arrived at the end of the Scripps pier, 16 miles north of San Diego, was 2.4 C lower than the sea surface temperature there. It was also lower than any known sea surface temperature in the near-by offshore area. Fog was observed at Lindbergh Field, San Diego, for 48 minutes beginning at 1820 PST. It retreated when the sea breeze, which had been WNW at 3 to 7 miles per hour, weakened and was replaced by S and E winds of 2 mph. The breakdown of the Pacific anticyclone into two cells occurred prior to 2235 PST, as shown by the synoptic weather map at that time.

Sounding C indicates the presence of a mixed layer below the inversion and is associated with fog at Lindbergh Field in the early morning and for a short period in the early evening. Careful measurements of sea surface and air temperatures were made at approximately half-hour intervals in the fog at distances 0.2 to 5.0 miles from shore on this day. Air temperature was observed at heights of a few inches, five feet, thirty feet, and seventy feet above the sea surface. Between 0950 and 1317 PST, when the observations were made, every air temperature was lower than the sea surface temperature. The average difference was 2.3 C.

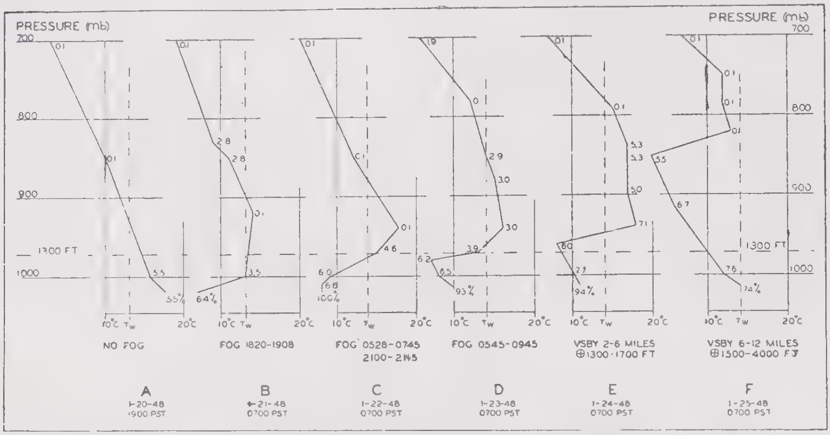

Figure 3. Soundings during the development of a fog situation, taken from radiosonde observations at North Island, San Diego, California. The number at the base of each sounding is the relative humidity. Other numbers along the soundings are specific humidities in grams per kilogram. Vertical lines are isotherms labeled at the base, and the dashed line, labeled T_w, is the sea surface temperature.

In sounding D the mixed layer has deepened but is still only 1,000 feet thick. On this day, which is typical of stage four in the model development, fog at Lindbergh Field formed at 0545 PST and lasted four hours. On the following day, January 24, the mixed layer became too deep for fog to form; visibilities were from two to six miles, and an overcast persisted all day with ceiling height from 1,300 to 1,700 feet. Thus the sequence ended. On the day represented by sounding F the highest temperature above the inversion had dropped below the sea surface temperature and the inversion base was too high to permit fog formation. Visibilities continued to improve and were from six to twelve miles. The sky remained overcast with ceilings from 1,500 to 4,000 feet.

NONDIURNAL INDICES OF FOG

In order to characterize the stage of the fog situation development where fog may be expected at Lindbergh Field, three nondiurnal indices have been defined. Each element used in determining values of the indices is measured at a given time of day. Thus diurnal variations do not affect the index values. So that a day would usually include both the formation and dissipation time of fog, a 'fog day' was defined as the period from 1630 PST on one calendar day through 1629 on the following calendar day. The indices for a given fog day are:

1. Height of the Inversion Base: The height above which the air temperature increases with height at the most rapid rate on the North Island (San Diego) morning raob (radiosonde observation).
2. Temperature Index: The quantity ($T_a - T_w$) where, if an inversion exists with base below 3,000 feet, T_a is highest air temperature above the inversion base on the morning raob or, if no inversion exists with base below 3,000 feet, T_a is the surface air temperature on the morning raob; T_w is the sea surface temperature at the end of the Scripps pier.[2]
3. Moisture Index: The quantity ($DP_{1630} - T_w$) where DP_{1630} is the surface dew point at Lindbergh Field at 1630 PST and T_w is the sea surface temperature on the preceding fog day.

Values of the three nondiurnal fog indices have been determined for each day of the period 1943 through 1945, when data were available. It was observed that most days on which fog occurred were days when the indices had values lying within certain ranges. Limits were placed on these ranges after a study of the variations. The ranges, determined to be favorable to fog, were: for height of inversion base, 0 to 1,300 feet; for temperature index, any positive value; for moisture index, any positive value or any negative value between 0 and -5 C.

The index ranges selected as favorable to fog in the winter period have been found to be applicable also to fogs which develop in the summer period. However, in summer the synoptic weather features which bring dry warm air over the sea and cause the inversion base to lower into the range favorable for fog may be different than in winter. Blake (2) has shown large-scale zonal subsidence to be an important process.

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[2] Regular sea surface temperature observations are not made closer to San Diego than the Scripps pier; however, selected observations have shown that the temperature at the pier is usually representative of the coastal regions closer to San Diego and in San Diego Bay.

In the period 1943–1945 there were 222 days when all three indices were favorable to fog; on 62 of these days (28%) fog (*i. e.*, visibility ½ mile or less) occurred. There were 825 days which did not favor fog because at least one index was unfavorable; on 23 of these days (2.8%) fog occurred. Thus, the percentage of fog occurrences on days defined by the indices as favorable to fog was ten times as great as the percentage of occurrences on unfavorable days. Furthermore, on the 23 days when fog occurred with unfavorable conditions existing at normal times for the determination of index values, linear interpolation (or allowance for observational error) shows that the indices were probably favorable at the time of fog formation. There was one exception, when a period of fog lasted only 40 minutes; this was associated with rapidly falling pressure and was followed by rain and strong frontal activity.

For practical purposes it may be stated that fog will not form at Lindbergh Field on a given day unless the three nondiurnal indices are favorable. These indices thus provide a necessary but not sufficient condition for fog formation. If the conditions are to become sufficient, other considerations must be employed. One which shows considerable promise is an evaluation of the effect of moisture in the atmosphere above the inversion base. In 1943, for example, there were 96 days favoring fog and 32 days when fog occurred. In that year, one when reliable moisture data were available, it was found that 47% of the 64 days favorable to fog but with no fog occurring were days when the moisture content aloft was high, as indicated by the mixing ratio at 10,000 feet being 3.5 grams per kilogram or greater. If 1943 is a typical year, then fog will form on 48% of the days having the three nondiurnal indices favorable and also having a mixing ratio at 10,000 feet less than 3.5. On the majority of the remainder of such days there will be a low overcast or a fog bank at sea.

The indices have been plotted against time over a three-year period. It appears that they vary in a relatively slow and consistent manner which may be forecast, and that they may be of value in day-by-day fog forecasting for Lindbergh Field. Since fog formation, wherever it may occur, is controlled by some of the same factors and processes which operate at San Diego, it may be possible to apply similar reasoning and indices to other locations.

ACKNOWLEDGMENT

The author wishes to express his appreciation to Dr. H. U. Sverdrup for encouragement and support in carrying out the work upon which this discussion is based. Mr. Dean Blake gave helpful advice based upon his forty-five years' experience in weather problems in the San Diego area. The local office of the U. S. Weather Bureau, the Naval Air Station, and the Navy Electronics Laboratory have furnished data and valuable co-operation.

SUMMARY

A model illustrating the manner in which fog situations develop in the winter period in the San Diego area is presented. The importance of the role played by sea surface temperature is stressed. An observed example of the development is described. Nondiurnal indices are defined, these serving as criteria to aid in determining whether or not fog will form at Lindbergh Field, San Diego, on a given day in either summer or winter.

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Contribution No. 382

NOTES ON A THEORY OF THE THERMOCLINE[1]

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INTRODUCTION

The very large number of bathythermograms which have been taken during the last few years have established the essential features of the temperature structure in the upper layers of the ocean. When these layers are heated during a period of calm, the bathythermograms show a marked temperature gradient all the way to the surface, as shown in Fig. 1. If subsequently a strong wind starts to blow, the upper layers are stirred until an almost homogeneous layer is formed, bounded beneath by a region of marked temperature gradient, the thermocline. The transition from the homogeneous layer to the thermocline is usually sudden. If the wind increases in intensity the thermocline moves downward, but the characteristic *shape* of the temperature-depth curve remains essentially unchanged.

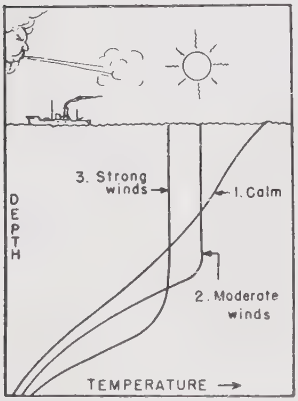

Figure 1. Schematic presentation of the development of a wind stirred layer and thermocline.

It has been customary to interpret the wind-stirring effect in terms of Ekman's famous theory for wind driven currents on a rotating globe (Ekman, 1905; Sverdrup, *et al.*, 1942: 492–494). Ekman assumes *homogeneous* water and a constant value[3] for the eddy

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[3] Ekman (1905) also gives a solution for the case where the eddy viscosity is proportional to the shear. This does not modify the essential meaning of our remarks.

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viscosity, and obtains for a solution current vectors whose azimuths vary linearly and whose magnitudes decrease exponentially with depth from the very surface downward. Therefore, the Ekman spiral does not contain the concept of a homogeneous upper layer with a well defined lower boundary. Nevertheless, this concept has often been brought in by means of the artifice of identifying the thickness of the mixed layer with a depth where the current equals $e^{-\pi}$ times the surface current and is directed opposite to it.

The difficulty can be resolved, at least qualitatively, by taking into account the effect of the density stratification on the scale of turbulence. Ekman (1905) stated:

> It is obvious that [the eddy coefficient] cannot generally be regarded as a constant when the density of the water is not uniform within the region considered. For [the eddy coefficient] will be greater within the layers of uniform density and comparatively small within the transition-layers where the formation of vortices must be much reduced owing to the differences of density.

The reduction in the vertical eddy conductivity in the thermocline leads to high resistance to heat flux from above, with ". . . the paradoxical result that the water-masses below . . . are the more 'protected' against heating the stronger the heating . . ." (Helland-Hansen, 1930: 44). Surface heating therefore tends toward sharpening the existing temperature gradient in the thermocline and further reducing the turbulence. At the same time, the reduction in turbulence permits relatively easy slippage of water layers with respect to one another, and the resulting shear in the thermocline represents a source for producing turbulent energy. The ultimate outcome must be a steady-state distribution which represents a balance between the stabilizing influence of temperature gradients and the unstabilizing influence of current gradients. It is this steady-state solution which is being sought.

The foregoing discussion indicates how intimately the problems of current and of temperature distributions are related. Mathematically they are linked by the coefficients of eddy viscosity and conductivity, both of which are functions of the gradients of temperature *and* current. For the eddy viscosity such a function has been introduced by Rossby and Montgomery (1935); for the eddy conductivity a new relationship will be derived. These functions will be substituted into the differential equations governing the distributions of temperature and current, and the differential equations solved *simultaneously*.

Ekman was well aware of the desirability of incorporating these thermodynamic considerations into his dynamic treatment of ocean currents. He wrote that ". . . this is however a complication which cannot be taken into account in the general theory . . ." We have been fortunate to have at our disposal the new Differential Analyzer of the University of California. With this computer, numerical solutions have been found for 21 examples; 14 examples correspond to actual conditions for which complete observational material was available, and which were in agreement with the assumptions underlying the theory. The most restrictive of these assumptions is that the net heat flux be directed downward and that there be no convective stirring such as might be induced by surface cooling due to evaporation.

EQUATIONS OF TURBULENT FLUX UNDER STABLE CONDITIONS

The downward flux, per unit area, of momentum, of heat and of salt, due to turbulent processes, equal respectively

$$F_M = -A_V V', \quad F_T = -c_p A_T T', \quad F_S = -A_S S', \qquad \text{(1 a, b, c)}$$

where c_p is the specific heat at constant pressure, A_V, A_T, and A_S the dynamic eddy coefficients (dimensions mass length^{-1} time^{-1}) of viscosity, conductivity and diffusivity, respectively. The accents (′) denote differentiations with respect to depth:

$$V' = \partial V/\partial z, \qquad T' = \partial T/\partial z, \qquad S' = \partial S/\partial z, \qquad (2)$$

positive z being directed downward. It is customary to refer to V' as shear and to

$$\tau = -F_M \qquad (3)$$

as stress.

The coefficients A_V, A_T and A_S are not physical constants of the fluid but depend upon the state of its motion and may vary with time and position. Two factors tend to reduce the values of the turbulence coefficients: boundaries and stable stratification. Since the effect of the boundary is limited to the upper few meters of the ocean, we shall be concerned only with stability.

Let the subscript "o" denote the case of *neutral stability*. The ratio A/A_o for any one of the three coefficients in equation (1) is assumed to depend explicitly on stability, shear and gravity:

$$A/A_o = f\,(E, V', g), \qquad (4)$$

where the stability E depends upon the temperature and salinity distributions

$$E = E\,(T', S', T, S), \qquad (5)$$

and these distributions vary with depth and time. The theory of the wind-stirred layer is contained in the solution $T(z)$ of equations (4), (5) and the three equations (1).

Stability, Temperature and Salinity Gradients. It is convenient, whenever possible, to express the stability as a function of temperature gradient or salinity gradient only:

$$E = a\,T' \qquad \text{or} \qquad E = b\,S'. \tag{6}$$

To examine the implications of equation (6) and to determine the coefficients a and b, we make use of equation XII, 12–14, in Sverdrup, *et al.* (1942), according to which

$$E = \frac{1}{\rho}\frac{\partial \rho}{\partial z} \doteq 10^{-3}\frac{\partial \sigma_t}{\partial z} \tag{7}$$

except at great depth. Expanding by partial differentiation one finds

$$E = 10^{-3}\left(\frac{\partial \sigma_t}{\partial T}\,T' + \frac{\partial \sigma_t}{\partial S}\,S'\right) = 10^{-3}\left(\frac{\partial \sigma_t}{\partial T} + \phi\,\frac{\partial \sigma_t}{\partial S}\right)\,T', \tag{8}$$

or

$$E = 10^{-3}\left(\frac{1}{\phi}\,\frac{\partial \sigma_t}{\partial T} + \frac{\partial \sigma_t}{\partial S}\right)S', \tag{9}$$

where, provided S and T are functions of z only,

$$\phi = \frac{S'}{T'} = \frac{dS}{dT} \tag{10}$$

is the slope of the line denoting the T-S relationship of the water mass. Comparison between equations (6) and (8) or (9) gives

$$a = 10^{-3}\left(\frac{\partial \sigma_t}{\partial T} + \phi\,\frac{\partial \sigma_t}{\partial S}\right), \quad b = 10^{-3}\left(\frac{1}{\phi}\,\frac{\partial \sigma_t}{\partial T} + \frac{\partial \sigma_t}{\partial S}\right). \tag{11}$$

To simplify computations, the parameters a or b will be considered independent of depth in subsequent integrations. This involves the assumptions that over the range of integrations the T-S relationship is linear, with variations in temperature and salinity small. The errors introduced by these assumptions are generally small compared to those inherent in Ekman's assumption of a constant eddy viscosity.

TABLE I. VALUES OF $\partial\sigma_t/\partial T$

T \ S	33°/oo	35°/oo	37°/oo
0 °C	−.045	−.055	−.060
10 °C	−.170	−.172	−.175
20 °C	−.260	−.262	−.265

TABLE II. VALUES OF $\partial\sigma_t/\partial S$

T \ S	33°/oo	35°/oo	37°/oo
0 °C	.806	.806	.807
10 °C	.779	.780	.780
20 °C	.760	.761	.763

Effect of Stability and Shear on Eddy Coefficients. According to the Π-theorem in dimensional analysis, the quantities E, V', and g, on which the ratio of eddy coefficients was assumed to depend (equation 4), can be combined into only one type of nondimensional number, the Richardson number r (Brunt, 1939: 237):

$$r = g\,E/(V')^2. \tag{12}$$

In selecting a particular functional relationship we are guided by the limiting conditions

$$A \rightarrow A_o \text{ for } r \rightarrow 0, \tag{13}$$

$$A \rightarrow 0 \text{ for } r \rightarrow \infty. \tag{14}$$

Equation (14) states that for very high stability the flux of momentum heat and salt takes place by molecular processes only.

A simple set of equations which satisfy (13) and (14) is

$$A_V = A_o\,(1 + \beta_V\, r)^{-n_V}, \tag{15}$$

$$A_T = A_o\,(1 + \beta_T\, r)^{-n_T} = A_S, \tag{16}$$

where the eddy coefficients for *neutral* stability

$$A_{V,\,o} = A_{T,\,o} = A_{S,\,o} = A_o \tag{17}$$

have been assumed equal,[4] and where β_V, n_V, β_T, n_T are positive constants, not yet determined. The coefficients pertaining to heat flux and salinity diffusion are assumed to equal one another but to differ from the coefficient pertaining to momentum flux (see below).

Equation (15) is a relationship derived by Rossby and Montgomery (1935). It will be shown that the constants in (16) can be evaluated from known relationships, and that the resulting equations are in agreement with observations.

DETERMINATION OF CONSTANTS

Application of Investigations by Rossby and Montgomery and by Sverdrup. From energy considerations, Rossby and Montgomery (1935) derived an equation identical in form to equation (15), with $n_V = \frac{1}{2}$. Sverdrup (1936), on the basis of his measurements over a snow field at Spitzbergen, estimates β_V at 10 to 13, and probably nearer the lower limit. We shall adopt the value $\beta_V = 10$.

---

[4] "In recent years a great deal of work on the relationship between A_S and A_V has been done in the field of Aeronautics. The assumption of Reynold and Prandtl that $A_S = A_V$ has been confirmed in all cases when the fluid is homogeneous" (Taylor, 1931, notation ours).

Jacobsen's Investigation. From his extensive analysis of salinity and current observations in Randers Fjord and Schultz Ground, Jacobsen (1913) postulates that under stable conditions the turbulent elements give off their momentum rapidly to their surroundings, whereas other properties, such as temperature and salinity, are exchanged slowly. The elements are therefore moved to new surroundings by gravitational forces before equalization can take place. As a consequence, ". . . the effect of stability on turbulence is two-fold. In the first place, the turbulence is reduced, leading to smaller values of the eddy viscosity, and, in the second place, the type of turbulence is altered in such a manner that the accompanying eddy diffusivity becomes smaller than the eddy viscosity" (Sverdrup, *et al.*, 1942: 477).

The first conditions, $A_V \leqslant A_o$, is already satisfied by equation (15); the implication of the other condition,

$$X_j \equiv A_S/A_V \leqslant 1, \tag{18}$$

remains to be investigated. Substituting from equations (15) and (16) gives

$$X_j = (1 + \beta_V r)^{n_V} (1 + m \beta_V r)^{-n_T}, \tag{19}$$

where

$$m = \beta_T/\beta_V. \tag{20}$$

For $r = 0$ one finds

$$X_j = 1,\ d X_j / d r = - \beta_V n_T (m - n_V/n_T), \tag{21}$$

so that

$$m \geqslant n_V/n_T, \tag{22a}$$

in order for Jacobsen's condition (18) to be satisfied (Fig. 2). The special case

$$m = n_V/n_T, \tag{22b}$$

for which X_j approaches 1 asymptotically as r approaches zero, seems more likely from a physical point of view than the general case for which $d X_j / d r$ has a finite value at $r = 0$.

For very large values of r,

$$X_j \doteq m^{-n_T} (\beta_V r)^{n_V - n_T}, \tag{23}$$

and

$$n_T \geqslant n_V, \tag{24}$$

in order for (18) to be satisfied. Equations (22) and (24) impose certain restrictions upon the numerical values of n_T and β_T.

Taylor's Investigation. Further restrictions are imposed by an entirely different condition proposed by Taylor (1931):

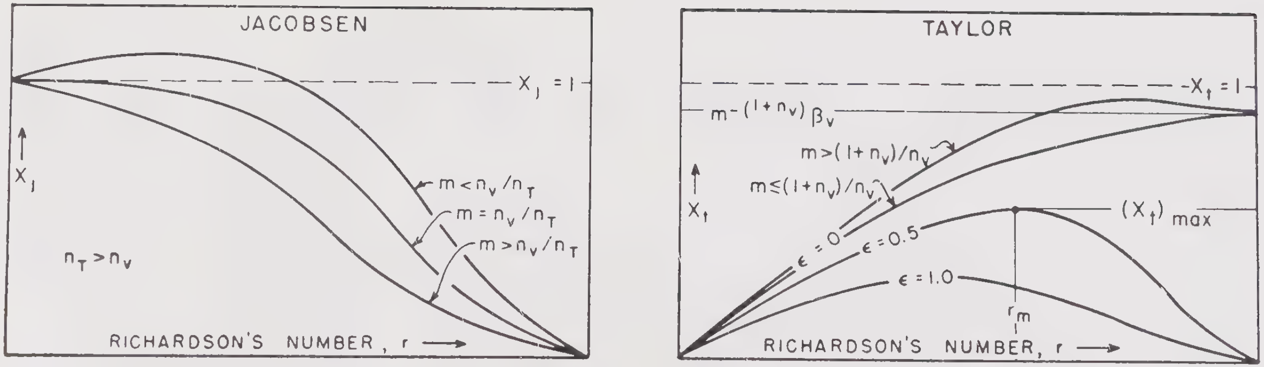

Figure 2. Limitations imposed by Jacobsen's and by Taylor's conditions upon the constants in equations (15) and (16). See text.

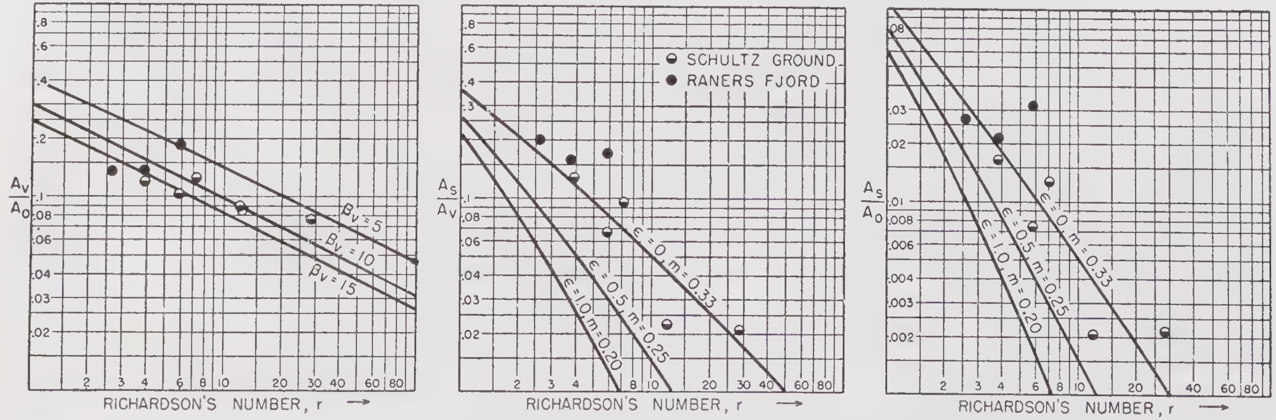

Figure 3. Comparison of theoretical relationships between eddy coefficients and Richardson's number with that derived from Jacobsen's observations of current and salinity. The left part of the figure confirms the value of βv obtained by Sverdrup from meteorological measurements over a snow field. The central and right parts are consistent with values of ϵ and m derived from physical considerations.

In the case of a stratified fluid with density increasing downward any disturbance to steady laminar flow necessarily involves an increase in gravitational potential energy. It is this increase which causes infinitely small disturbances of a fluid at rest to be stable. In cases of turbulent flow the rate at which energy flows into a layer of the fluid owing to the action of the fluid above and below it must be greater than the rate at which gravitational energy increases in the same portion of the fluid.

Taylor shows that the fraction of available energy which is used to increase gravitational potential energy equals $r\,A_T/A_V$, and his argument requires therefore that

$$X_t \equiv r\,A_T/A_V \leqslant 1. \tag{25}$$

Again returning to (15) and (16) one finds

$$X_t = r\,(1 + \beta_V\,r)^{n_V}\,(1 + m\,\beta_V\,r)^{-n_T}. \tag{26}$$

For very small values of r, equation (26) reduces to $X_t \doteq r$, independent of β_T and n_T (Fig. 2). For large values of r,

$$X_t \doteq m^{-n_T}\,\beta_V{}^{n_V - n_T}\,r^{1+n_V-n_T}, \tag{27}$$

so that $n_T \geqslant 1 + n_V$, or

$$n_T = 1 + n_V + \varepsilon, \quad \varepsilon \geqslant 0, \tag{28}$$

in order for Taylor's condition (25) to be satisfied.

In general X_t reaches a maximum, to be designated by $(X_t)_{\max}$, for $r = r_m$ (Fig. 2), where r_m is a root of the equation

$$m\,\varepsilon\,\beta_V{}^2\,r_m{}^2 + \beta_V\,[m\,(n_V + \varepsilon) - (1 + n_V)]\,r_m - 1 = 0. \tag{29}$$

As long as Taylor's condition holds for $(X_t)_{\max}$ it certainly must hold for any other values of X_t, and we may express equation (25) in the more definite form

$$(X_t)_{\max} \leqslant 1. \tag{30}$$

For the special case

$$\varepsilon = 0, \text{ and } m \leqslant (1 + n_V)/n_V, \tag{31}$$

a true maximum does not exist, but X_t remains bounded (Fig. 2). The term $(X_t)_{\max}$ in equation (30) is then interpreted as $m^{-(1+n_V)}\,\beta_V{}^{-1}$, the value of X_t at $r = \infty$. The special conditions stated in equation (31) appear more reasonable than any of the other possible combinations, as these other combinations require that, with increasing stability, the fraction X_t of the available energy going into potential energy should first increase and then decrease.

Equations (28), (29), and (30) define a minimum value for m for any fixed value of ε. Limitations imposed by Jacobsen's and by Taylor's conditions on the constants n_T and β_T are summarized in Table III.

Taylor's condition imposes the more severe restriction on n_T, whereas Jacobsen's condition imposes the more severe restriction on m, or β_T.

TABLE III. LIMITS TO CONSTANTS IMPOSED BY JACOBSEN'S AND BY TAYLOR'S CONDITIONS

Constant	n_V	n_T		ε	n_T	m	
Source	Rossby	Jacobsen	Taylor	Assumed	——	Jacobsen	Taylor
Equation	—	(24)	(28)	—	(28)	(22a)	(28) (29) (30)
Values	0.5	$\geqslant 0.5$	$\geqslant 1.5$	0.0*	1.5	$\geqslant 0.33$†	$\geqslant 0.22$
—	—	—	—	0.5	2.0	$\geqslant 0.25$	$\geqslant 0.10$
—	—	—	—	1.0	2.5	$\geqslant 0.20$	$\geqslant 0.07$

* Preferable for reasons stated following equation (31).

† $m = 0.33$ preferable to $m > 0.33$ for reasons stated following equation (22b).

For reasons referred to in the footnotes to Table III, the combination

$$\varepsilon = 0,\ n_T = 1.5,\ m = 0.33 \tag{32}$$

appears to be the most reasonable. Substituting from (15) and (16) gives

$$\begin{aligned} A_V &= A_o\,(1 + \beta_V\, r)^{-1/2},\ \beta_V = 10 \\ A_S = A_T &= A_o\,(1 + \beta_T\, r)^{-3/2},\ \beta_T = \beta_V/3 = 3.33\,. \end{aligned} \tag{34}$$

Some Numerical Values. Taylor (1931) has used Jacobsen's observations to test the validity of his criterion, and he finds condition (25) satisfied. The same observations have been used in Fig. 3, eliminating, however, the observation at 15 meters, where the shear shows a sudden change from neighboring depths which is inconsistent with the general trend.

The left part of Fig. 3 indicates the validity of equation (15), using $\beta_V = 10$. It has already been stated that this value was derived from meteorological observations; its applicability to oceanographic data may indicate that β_V represents a universal constant. The curves in the middle and right parts of Fig. 3 were computed for three values of ε and the corresponding *minimum* values of m (second column from right in Table III.) Increasing m shifts the curves toward the left away from the observations. The empirical data are consistent with the choice of values proposed in equation (32) on the basis of physical reasoning.

THE DISTRIBUTIONS OF VELOCITY AND TEMPERATURE

General Solution. The problem consists of solving simultaneously the five equations

$$\tau = A_V\, V', \qquad F_T = -\, c_p\, A_T\, T', \tag{1a, b}$$

$$A_V = A_o\,(1 + \beta_V\, r)^{-1/2}, \quad A_T = A_o\,(1 + \beta_T\, r)^{-3/2} \tag{33, 34}$$

$$r = g\, a\, T'\,(V')^{-2} \tag{35}$$

in the five unknowns V, T, A_V, A_T and r. Solving for r gives

$$\frac{g\,(-a)\,F_T\,A_o}{c_p\,\tau^2} = r\,(1 + \beta_V\, r)\,(1 + \beta_T\, r)^{-3/2}, \tag{36}$$

where, in general, a, F_T, A_o, and τ are all functions of z, and these functions must be specified in order that solutions $r = r\,(z)$ can be found. It will be convenient to introduce functions K and R so that equation (36) becomes

$$K\,(z) = R\,(r). \tag{37}$$

The distributions of velocity and temperature are best expressed in terms of r;

$$\frac{V'}{V_o'} = \frac{(1 + \beta_T\, r)^{3/4}}{r^{1/2}}, \quad V_o' = \frac{g\,(-a)\,F_T}{c_p\,A_o}, \tag{38}$$

$$\frac{T'}{T_o'} = (1 + \beta_T\, r)^{3/2}, \quad T_o' = -\frac{F_T}{c_p\,A_o}. \tag{39}$$

The above relationships are plotted in Fig. 4.

Depth and Sharpness of Thermocline. Before taking up the special case of the Ekman spiral, a few quite general remarks concerning the character of the thermocline can be made. These remarks are applicable to transient as well as steady-state conditions.

Two features which are usually prominent on bathythermograms are: (a) the maximum temperature gradient, $T' = T_{\text{max}}'$ at depth $z = z_g$; (b) the "knee," $T'' = T_{\text{max}}''$ at depth $z = z_c$. As a simple case, assume T_o' independent of z. It can be seen from Fig. 4 that in order for the temperature gradient to have a maximum value, r and hence $K\,(z)$ must reach a maximum. Other factors remaining equal, *the stress must be at a minimum where the temperature gradient is at a maximum. The maximum temperature gradient will be the larger, the smaller the value of the minimum stress.*

At the depth z_c of maximum curvature $T''' = 0$, or, according to (39),

$$r'' + (\tfrac{1}{2})\,\beta_T\,(1 + \beta_T\, r)^{-1}\,r'^2 = 0. \tag{40}$$

Combining this with the equations

$$K' = \frac{dR}{dr} r' , \tag{41}$$

$$K'' = \frac{d^2R}{dr^2} r'^2 + \frac{dR}{dr} r'' , \tag{42}$$

and substituting $\beta_T = \beta_V/3$, gives, after much manipulation,

$$K'' + QK'^2 = 0, \tag{43}$$

where

$$Q = \frac{2\,\beta_V\,(1 + \beta_T\,r)^{3/2}\,(\beta_V^2\,r^2 + 16\,\beta_V\,r - 15)}{(\beta_V^2\,r^2 + 11\,\beta_V\,r + 6)^2} \tag{44}$$

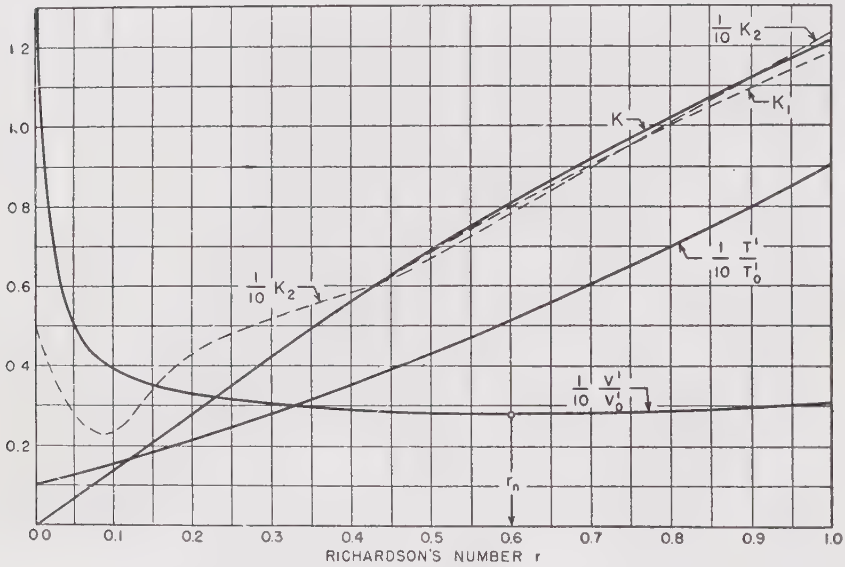

Figure 4. Plot of shear, temperature gradient, and the parameters K, K_1 and K_2 (see text) as functions of Richardson's number r. The shear reaches a minimum for $r = 0.6$.

is a function of r, or in view of (37), a function of K. The solution to (43) is

$$K_1 = C_1\,z + C_2, \tag{45}$$

where

$$K_1 = \int e^{-\int Q dK} dK$$

has been plotted in Fig. 4. Except for large values of r, $K_1 \doteq K$. *Therefore the depth* z$_c$ *of maximum curvature in the* T(z) *curve equals approximately the depth of zero curvature in the* K(z) *curve.*

The maximum curvature can be computed from

$$T_{\text{max}}'' = 3/2\ \beta_T\ (1 + \beta_T\ r)^{1/2}\ r'.$$

According to (40) and (45)

$$r' = \frac{K'}{R'} = \frac{C_1\, e^{\int Q dK}}{R'}$$

and

$$T_{\text{max}}'' = K_1'\ (z_c)\ K_2\ (z_c), \tag{47}$$

where

$$K_2 = \frac{(3/2)\ \beta_T\ (1 + \beta_T\ r)^{1/2}\ e^{\int Q dK}}{R'} \tag{48}$$

is plotted in Fig. 4. Thus if $K(z)$ is known, the depth of the thermocline and the sharpness of the "knee" on the temperature-depth curve can readily be computed.

Minimum Shear Layer. The shear reaches a minimum value

$$V'_{\text{min}} = \left[\frac{3\sqrt{3}}{2}\ \frac{g\ (-a)\ F_T\ \beta_T}{c_p\ A_o}\right]^{1/2} \tag{49}$$

when

$$r = r_n = 2/\beta_T = 0.6. \tag{50}$$

The corresponding values of A_V/A_o, A_T/A_o and K are 0.38, 0.19, and 0.81 respectively. The region of minimum shear occurs somewhat above the thermocline (Fig. 6). At greater depths the shear is larger because of the high stability which permits relatively easy slippage of water layers with respect to one another; at lesser depths the shear is larger because of the driving effect of the wind. Measurements to determine the possible existence of a minimum shear layer could serve as a critical test of this theory, especially as no corresponding feature is contained in Ekman's solutions.

The Modified Ekman Spiral. For steady-state conditions, with the frictional force balanced by the Coriolis force, the equations of motion take the form

$$\begin{aligned} \tau_x' &= \frac{d}{dz}\ (A_V\ V_x') = -\ C\ V_y \\ \tau_y' &= \frac{d}{dz}\ (A_V\ V_y') = C\ V_x\ , \end{aligned} \tag{51}$$

where

$$C = 2\omega \sin \varphi,$$

ω being the earth's rotational velocity, and φ the latitude, and where

$$\tau = \tau_x^2 + \tau_y^2, \qquad V' = V_x'^2 + V_y'^2, \qquad V = V_x^2 + V_y^2 \quad (52)$$

are the magnitudes of the stress, shear and velocity vectors, respectively. Equations (51) are identical in form with those solved by Ekman, the difference being that here A_V is a function of temperature gradient and shear, whereas Ekman treated A_V as constant, or a function of shear only.

Solutions were obtained by solving equations (1), (33), (34), (35) and (51) simultaneously on the differential analyzer. In order to have steady-state temperature distribution, the heat flux F_T was assumed independent of depth.

At the surface we set, with Ekman,

$$\tau_x = 0, \ \tau_y = - \tau_a \qquad \text{for } z = 0, \quad (53)$$

where τ_a is the stress of the wind on the sea surface, assuming the wind to blow along the positive y-axis. At great depths the only reasonable boundary condition is the one prescribed by Ekman, namely that the velocity vanishes. This condition cannot be reconciled with the existence of a minimum value for the velocity gradient unless the heat flux vanishes at great depth (equation 49). It appears that the distribution of temperature and current cannot both be stationary at the same time.

Without the bottom boundary conditions the solutions to the equations are no longer uniquely determined. To make the problem definite, we shall assume the components of surface current to be given by Ekman's equations

$$V_x = V_y = \frac{\tau_a}{\sqrt{2 \rho A_o C}} \text{ for } z = 0. \quad (54)$$

Values of A_o and τ_a as functions of the wind speed were read off Fig. 5.

The former are based on a comparison of Ekman's theory with observations (Sverdrup, *et al.*, 1942: 494), the latter on recent calculations[5] taking into account the roughness of the sea surface and the gustiness of the wind.

Fig. 6 shows the results of a sample calculation (run 3b, Table IV). Minimum shear is found at a depth of 15 meters, the maximum

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[5] A discussion by Mr. T. Saur is in preparation.

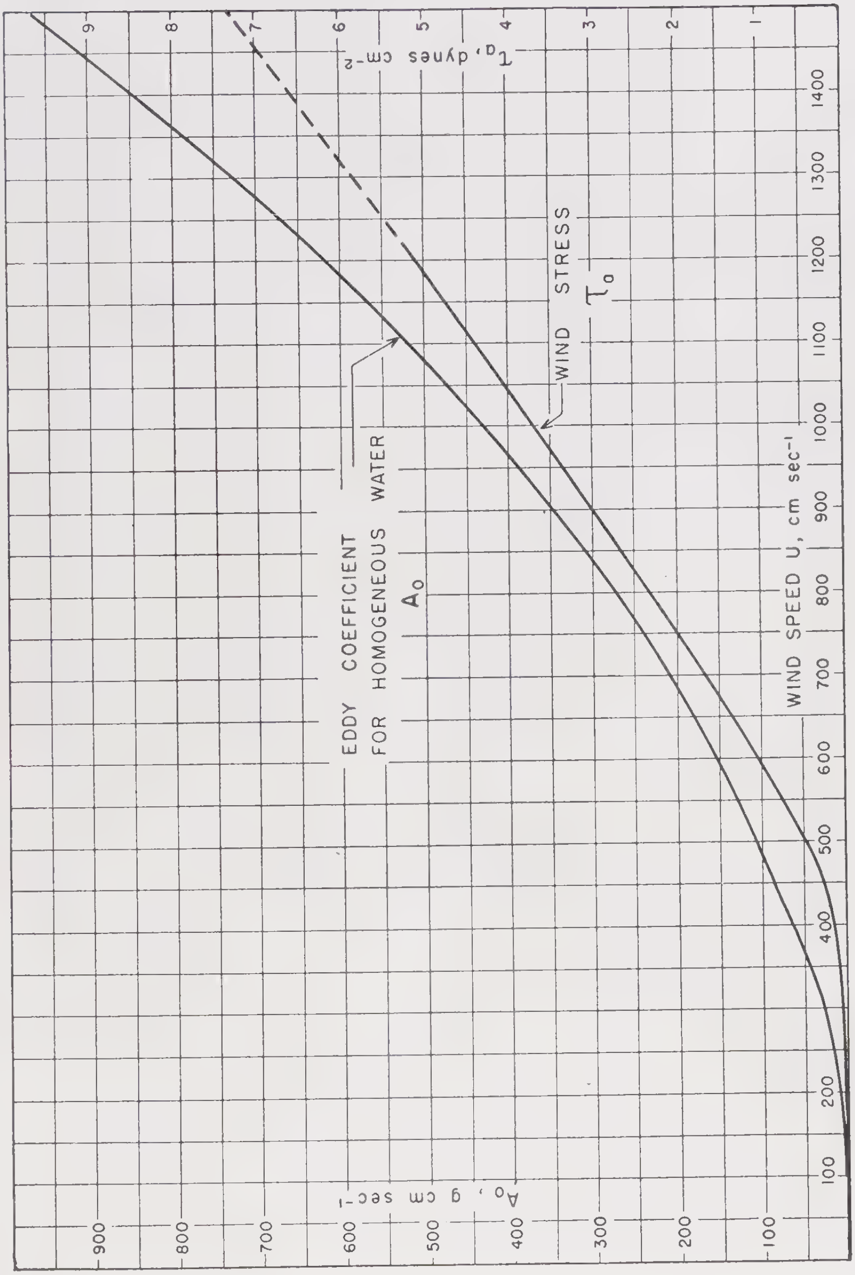

Figure 5. Relationships between wind speed at standard anemometer elevations, the wind stress per unit area of sea surface, and the eddy coefficient for homogeneous water.

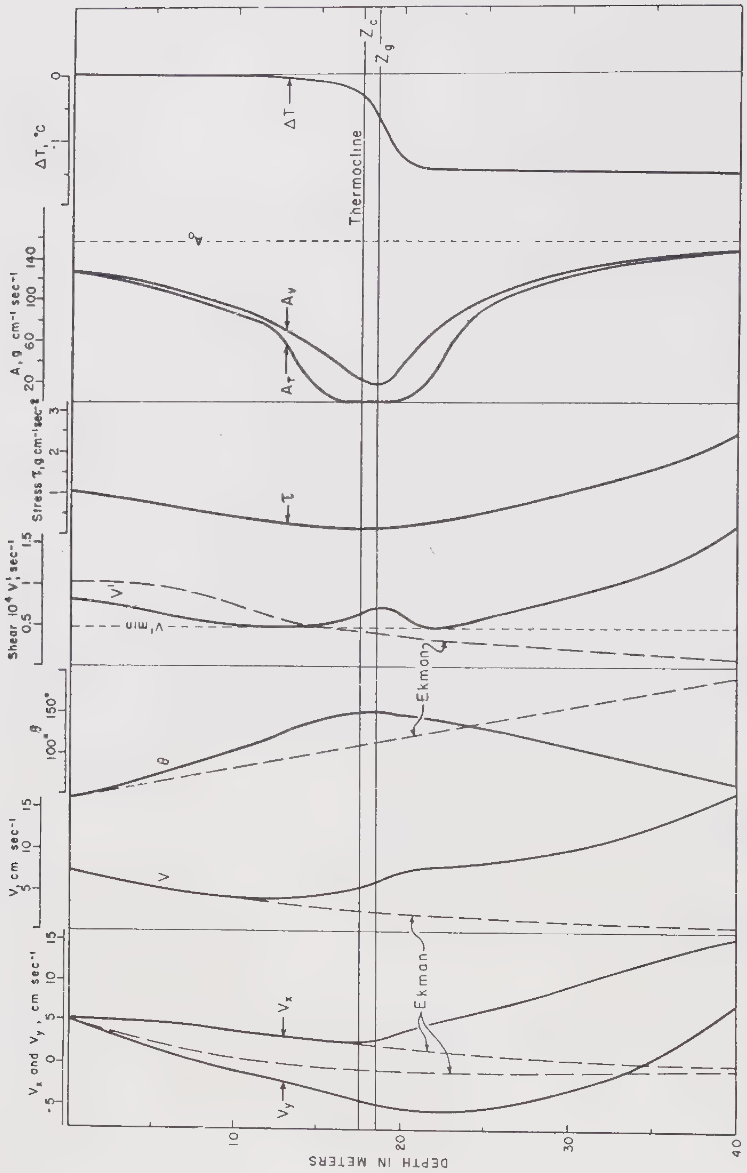

Figure 6. Results of computation on Differential Analyzer for Run 3b, Table IV.

curvature in the temperature depth curve at 17.5 meters, and the maximum temperature gradient at 18.5 meters. At the latter depth the stress reaches a minimum as predicted by the general theory.

Because of the simplifying assumption that F_T is a constant, the solution becomes increasingly inadequate the greater the depth.

Variation in Parameters. All parameters entering the differential equations and, according to our theory, the distributions of temperature and current in the upper layers of the oceans, depend upon four factors: the wind speed U, heat flux F_T, latitude φ, and the T-S correlation factor a. Some of these factors enter the equations more than once; U enters in three places. To determine the role played by each factor, computations have been carried out for typical conditions, varying one factor at a time.

The first five lines in Table IV show the results of the computations. Doubling the wind speed lowers the thermocline from 22 to 61 meters! Other factors have a much smaller effect. Doubling the latitude raises the thermocline by 40%, doubling the heat flux by 20%, doubling a by only 15%.

The next two lines in Table IV indicate that the computed depth of the thermocline does not depend critically upon the assumptions made in equation (54) as to the relative direction and velocity of the surface current.

COMPARISON WITH OBSERVATIONS

In selecting specific cases to be used for comparison with theory the following considerations were involved: (1) bathythermograph observations must be adequate; (2) evaporation relatively small; (3) heat flux positive; and (4) advection small, *i. e.*, no strong currents. The depth of thermocline was computed for: (1) a relatively clear-cut situation observed from a weather ship; (2) a broad strip in mid-Pacific, for which the computed and observed changes of thermocline depth with *latitude* could be compared; and (3) a lake at various times of the year, for which the computed and observed changes with *season* could be compared. Results are summarized in Table IV.

The weather ship was located at Lat. 49° 50′ N, Long. 145° 30′ W; the time of observation was September 28–29, 1943. Five bathythermographs taken during the 20-hour period were averaged to minimize the effect of internal waves. During this time interval there was condensation on the sea surface. The heat flux was computed from the general heat budget, following the method described on pp. 100–124 of Sverdrup, *et al.* (1942). The constant a was obtained from a hydrographic station occupied by the USS Bushnell on August 19, 1934, at Lat. 49° 29′ N, Long. 174° 31′ W. The observed depth of maximum curvature of the bathythermogram

TABLE IV. SUMMARY OF COMPUTATIONS ON DIFFERENTIAL ANALYZER

Run Number	*Wind Speed*	*Latitude*	*Heat Flux*	T–S *Correlation*	*Surface Speed*	*Wind Angle*	*Wind Stress*	*Eddy Viscosity*	*Depth z in Meters*		
	U (cm sec^{-1})	φ	$10^3 F_T$ (cal cm^{-1} sec^{-1})	$10^4 a$ (°C)$^{-1}$	$(v)_{z=0}$ (cm sec^{-1})	θ	τ (dynes cm^{-2})	A_0 (g cm^{-1} sec^{-1})	*Minimum Shear*	*Thermocline ($T''' = 0$) Computed*	*Observed*
	Variation of Parameters										
1h	600	30° N.	2.00	2.00	9.60	45.0°	1.02	155.0	19.6	22.0	—
2a	1200	30	2.00	2.00	24.30	45.0	5.15	619.0	58.9	61.0	—
3a	600	60	2.00	2.00	9.60	45.0	1.02	155.0	—	14.0	—
4	600	30	1.00	2.00	9.60	45.0	1.02	155.0	22.8	26.5	—
5	600	30	2.00	4.00	9.60	45.0	1.02	155.0	14.7	19.0	—
1j	600	30	2.00	2.00	9.60	48.4	1.02	155.0	18.1	21.5	—
3b	600	60	2.00	2.00	7.30	45.0	1.02	155.0	13.5	17.5	—
	Weather Ship (September, 1943)										
6	630	49	3.89	2.18	8.75	45.0	1.20	171.0	13.8	16.2	38.0
	Mid-Pacific NW–SE Strip (Average Summer)										
7	617	15	0.49	2.85	14.25	45.0	1.12	164.0	38.6	44.0	76.0
17	505	21	0.76	2.85	6.58	45.0	0.50	110.0	15.5	20.0	43.0
13	530	24	0.97	2.80	7.45	45.0	0.63	121.0	15.0	19.0	48.0
18	462	28	1.32	2.65	3.91	45.0	0.31	91.8	6.5	11.0	33.0
8	365	32	1.73	2.72	2.59	45.0	0.16	49.6	—	5.6	19.0
15	440	38	2.04	2.80	2.78	45.0	0.24	83.2	—	6.3	14.0
19	440	43	2.10	2.60	2.64	45.0	0.24	83.2	0.5	6.0	17.0
9	542	48	2.14	2.43	5.90	45.0	0.69	126.0	10.0	13.0	27.0
	Sweetwater Lake (April, May, June, July, August)										
10	350	32	1.18	1.89	2.58	45.0	0.15	43.7	3.5	7.2	6.5
14	330	32	2.28	2.07	2.63	45.0	0.14	36.6	—	4.5	6.5
11	365	32	2.00	1.33	2.59	45.0	0.16	49.6	2.3	7.5	5.5
16	325	32	2.20	2.23	2.50	45.0	0.13	35.0	—	3.0	4.0
12	300	32	1.18	1.83	2.39	45.0	0.11	27.5	2.3	4.5	4.0

trace was at 38 meters, the computed depth at 16 meters, giving a ratio of 0.43.

Computation for a mid-Pacific NW-SE strip was made for the summer season, during which evaporation is relatively small. The region is shown in the inset of Fig. 7. Values of a were computed from

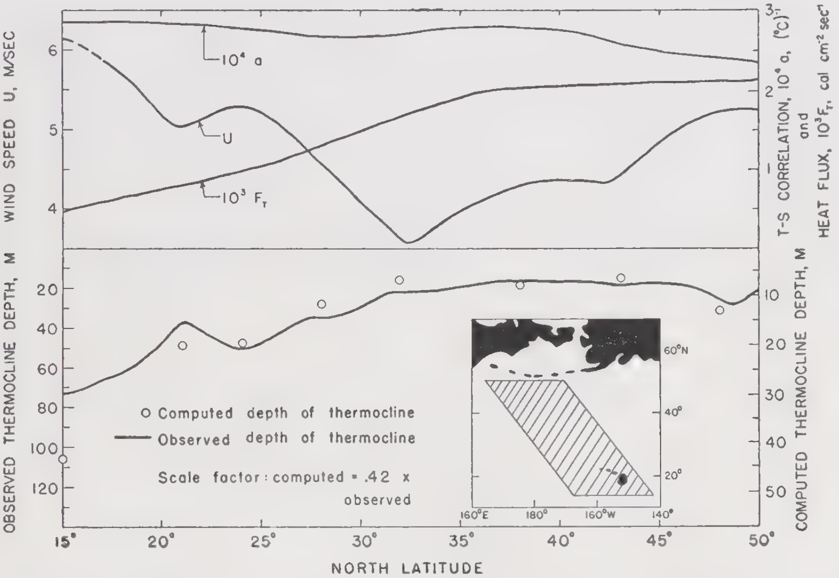

Figure 7. Comparison between computed and observed depths of thermocline as functions of latitude for the broad strip in the mid-Pacific shown in inset. The upper part gives the variations of the basic parameters entering the calculations.

selected USS Bushnell hydrographic stations. Wind speeds were obtained from pilot charts of the North Pacific. Values of heat flux for each five-degree square were kindly put at our disposal by Dr. W. C. Jacobs. These were computed on the basis of energy budget considerations, and they may be considerably in error because of uncertainties involved in some of the data. The observed depths of the thermocline were taken from a compilation by Mr. E. C. LaFond, using all data available prior to January 1945. For the extreme northern and southern portions of the area, the averages were adjusted for recent observations. Fig. 7 shows the variation with latitude of the basic parameters and of the observed and computed depths of thermocline. The computed depth is much too shallow, bearing roughly the same ratio to the observed depth as was found for the weather ship. Except for the southernmost station, the percentage *variations* in the depth of thermocline are similar for the computed and observed values.

Observations for Sweetwater Lake, California, taken during 1944 and 1945, have kindly been placed at our disposal by Mr. B. E. Holtsmark. Temperature observations were taken from a barge in water of about 50-foot depth. No wind observations were taken at the time, and it has been necessary to use wind data taken at Lindberg Field, San Diego, located approximately 12 miles from Sweetwater Lake. Values of a were obtained from standard tables of density of fresh water at various temperatures. The heat flux, which was computed by Mr. Holtsmark, using the energy budget method, was positive during the months under consideration. The agreement between the computed and observed depths of thermocline is fairly good. In addition, computations revealed an appreciable temperature gradient from the very surface downward, a feature in agreement with observations.

CONCLUSIONS

In view of the difficulty experienced in selecting conditions under which heat loss by evaporation is relatively small compared to heat gain by radiation, it would appear that convective stirring is as important as wind stirring in many, and perhaps most, cases. Therefore, it would be preferable to refer to the upper mixed layer by a less implicating term than "wind stirred layer."

The present model is greatly over-simplified. The effects of convective stirring, and of the convergence and divergence of the horizontal current field, must exert predominant influences in certain regions. If the heat flux had been assumed to decrease quasi-exponentially with depth, to take into account the absorption of radiation, more consistent results would have been obtained. In view of the close inter-relation between the temperature and current distributions, the turbidity of the water might be an important factor in the dynamics of wind currents.

Except in the case of Sweetwater Lake, where the winds were quite low, the computed depths of the thermocline are somewhat less than half the recorded depths. Perhaps this discrepancy is due to the assumed relationship $A_o(U)$ (Fig. 5) for the eddy coefficient under *indifferent* equilibrium which is based largely on measurements made when the density stratification was stable.

It has been demonstrated: that the sharp transition between the mixed layer and the thermocline can be accounted for theoretically by letting the eddy coefficients be functions of the stability and shear;

that the theory gives a thermocline depth which, although too shallow, is of the right order of magnitude; that this depth depends on wind speed, latitude, heat flux, and the *T-S* correlation, in the order stated, and that the variation with each of these factors occurs in a reasonable direction.

ACKNOWLEDGMENTS

We are indebted to Messrs. W. C. Jacobs, E. C. LaFond and B. E· Holtsmark for permission to use some of their unpublished data· Messrs. R. L. Stoker and E. Janssen of the Differential Analyzer Service, Department of Engineering, University of California at Los Angeles, have been helpful beyond what was involved in setting up the problem on the analyzer. Dr. L. Lek carried out some of the numerical computations, but unfortunately circumstances did not permit him to take a more active part and to join us in submitting this paper in appreciation to Dr. H. U. Sverdrup for having taught us oceanography.

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Contribution No. 383

THE DYNAMICS OF LARGE HORIZONTAL EDDIES (AXES VERTICAL) IN THE OCEAN OFF SOUTHERN CALIFORNIA[1]

By

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INTRODUCTION

A striking feature shown on charts of horizontal circulation of the ocean in the southern California region, Lat. 32° to 34.5° N., is a large counterclockwise eddy between a northward inshore current and a southward offshore current. Charts arranged in time order from spring, at intervals of about two weeks, show a decrease in velocity and an increase in size of the eddy. This suggests that these eddies may be successive stages in the decay of an initial state of maximum intensity and relatively small extent. In order to simplify the dynamical problem thus presented, equivalent circular eddies are derived by averaging the velocities of the actual oval-shaped ones.

Each of three series of such circular eddies conformed approximately to the principle of the conservation of angular momentum, and the kinetic energy was found to decrease according to a formula of the dissipation of energy caused by lateral eddy viscosity. Values of the coefficient of eddy viscosity computed by means of this formula ranged from 3×10^4 to 6×10^5 c. g. s.

A combination of the two general hydrodynamic differential equations of horizontal motion in the sea, involving the deflecting force due to the earth's rotation as well as pressure gradient and lateral turbulence, led to a single differential equation of the diffusion of vorticity. A solution of this equation was found corresponding to constant initial vorticity over a circular area of appropriate radius

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[2] It is a pleasure to acknowledge the help of Hector Venancio Iglesias, Lt. Comdr. in the Argentine Navy, one of my students, for his skillful execution of various supplementary computations that involved methods of interpolation, differentiation and integration.

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and zero vorticity outside of this area. Application of Stokes theorem (Lamb, 1945: 31–36) relating circulation to vorticity provides a means of computing the velocity corresponding to any time and distance from the center of the eddy. Substituting in this expression for velocity the value of the coefficient of eddy viscosity (found from the rate of energy dissipation) and a value of the initial radius (estimated from an inspection of the charts) yields the theoretical velocity except for a constant factor. This factor, which is also the maximum initial velocity, was determined by comparison of the values of the foregoing expression with the velocities at the earliest date of observations in each series. Thus the velocity-distance relation can be predicted for any later time. The general agreement of the mathematical model with observations materially reinforces the evidence in support of the thesis suggested by an inspection of current charts arranged according to time.

THE HORIZONTAL CIRCULATION OFF SOUTHERN CALIFORNIA INFERRED FROM DYNAMIC HEIGHT ANOMALIES ACCORDING TO THE BJERKNES METHOD

The charts of horizontal circulation (Figs. 1 to 10) off southern California show certain striking features typical of this region. They are a selection based upon systematic seasonal surveys (Sverdrup and Staff, 1938: charts on pp. 14, 16, 17, 19, 21; 1939: charts on pp. 68, 69, 71–75; 1940: MS. charts; 1941: charts on pp. 250–264) made in collaboration with the California State Fish and Game Commission. Attention is called especially to the large counterclockwise eddies, centered at about Lat. 33.5° N. and Long. 119.5° W., which form a striking part of the general circulation pattern of prevailing northward inshore currents and southward offshore currents. Although recognized by various oceanographers, these eddies have not been the subject of detailed investigation. An inspection of Figs. 1 to 5, showing the circulation at the 50-meter level during 1940, suggests a succession of stages of an eddy of maximum initial intensity and relatively small extent. This percept is also suggested by Figs. 6 to 10 showing the surface circulation during 1941, although the period of observation is about two months later and although the first eddy has a larger area than that of 1940. In order to simplify the problem and to emphasize the essential characteristics, equivalent circular eddies were obtained by averaging the velocity between each pair of streamlines and averaging the distances to the center of the actual oval-shaped eddy. Figs. 11 to 14 show such equivalent circular eddies at the surface for 1940, and Figs. 15 to 18, for the same year, show equiva-

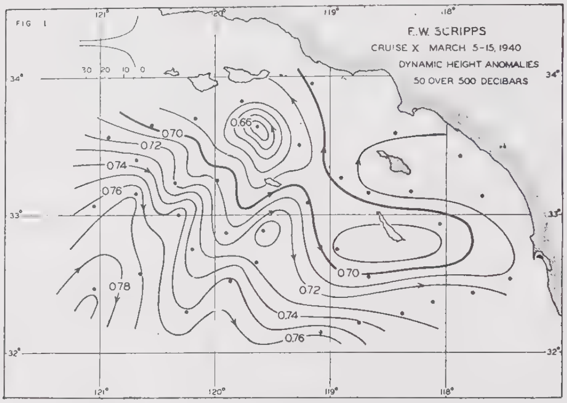


FIG 1
E.W. SCRIPPS
CRUISE X MARCH 5-15, 1940
DYNAMIC HEIGHT ANOMALIES
50 OVER 500 DECIBARS
121°
120°
119°
118°
34°
33°
32°
30 20 10 0
0.66
0.70
0.72
0.74
0.76
0.78
0.70
0.72
0.74
0.76

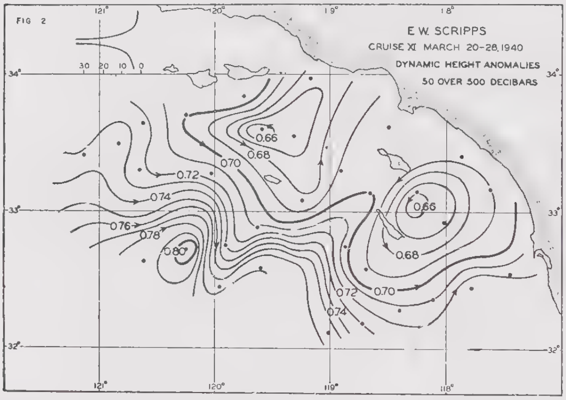


FIG 2
E.W. SCRIPPS
CRUISE XI MARCH 20-28, 1940
DYNAMIC HEIGHT ANOMALIES
50 OVER 500 DECIBARS
121°
120°
119°
118°
34°
33°
32°
30 20 10 0
0.66
0.68
0.70
0.72
0.74
0.76
0.78
0.80
0.66
0.68
0.70
0.72
0.74

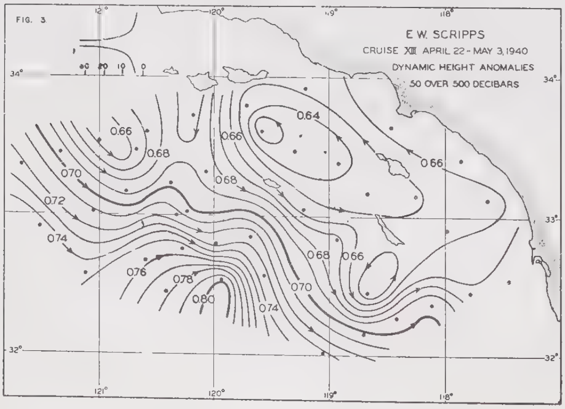


FIG. 3
E.W. SCRIPPS
CRUISE XIII APRIL 22 - MAY 3, 1940
DYNAMIC HEIGHT ANOMALIES
50 OVER 500 DECIBARS
121°
120°
119°
118°
34°
33°
32°
40 30 10 0
0.64
0.66
0.66
0.68
0.66
0.68
0.70
0.72
0.74
0.68
0.66
0.76
0.78
0.80
0.70
0.74

Figures 1–3. Dynamic Height Anomalies (current boundaries) 50 over 500 Decibars, 1940 lent circular eddies at the 50-meter level. The average velocity between each pair of circles is inversely proportional to the distance between them, according to the Bjerknes theory. The simplest curves showing the relation of velocity to distance from the center, corresponding to each circular eddy, are shown by the heavy lines in the same figures. In general, the curves show that the velocity increases from zero at the center of the eddy to a maximum, and then decreases. The position of maximum velocity of the surface eddy, at the earliest date, is about 12 kilometers from the center and shifts farther from the center at later stages. The eddy at the 50-meter

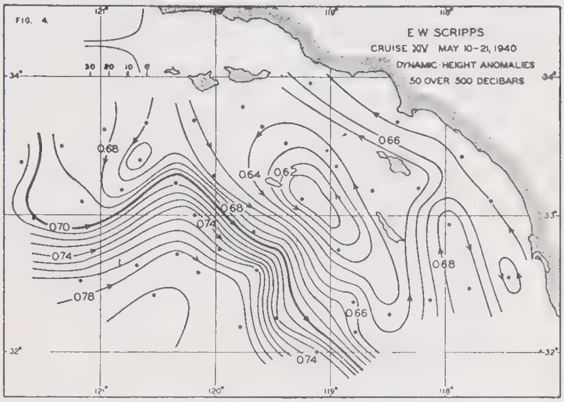


FIG. 4
E W SCRIPPS
CRUISE XIV MAY 10-21, 1940
DYNAMIC HEIGHT ANOMALIES
50 OVER 500 DECIBARS
121°
120°
119°
118°
34°
33°
32°
30
20
10
0
0.68
0.64
0.62
0.66
0.68
0.74
0.70
0.74
0.78
0.68
0.66
0.74

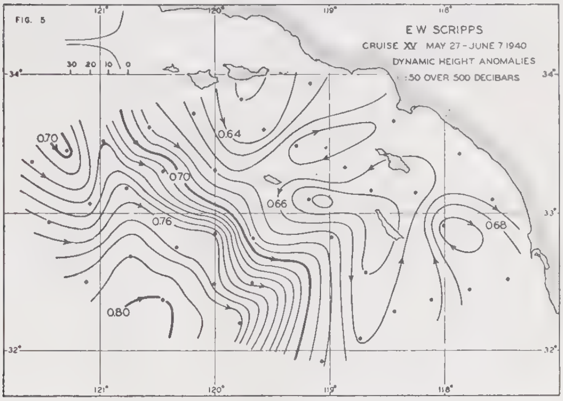


FIG. 5
E W SCRIPPS
CRUISE XV MAY 27-JUNE 7 1940
DYNAMIC HEIGHT ANOMALIES
50 OVER 500 DECIBARS
121°
120°
119°
118°
34°
33°
32°
30
20
10
0
0.70
0.64
0.70
0.66
0.76
0.68
0.80

Figures 4, 5. Dynamic Height Anomalies (current boundaries) 50 over 500 Decibars, 1940.

FIG 6

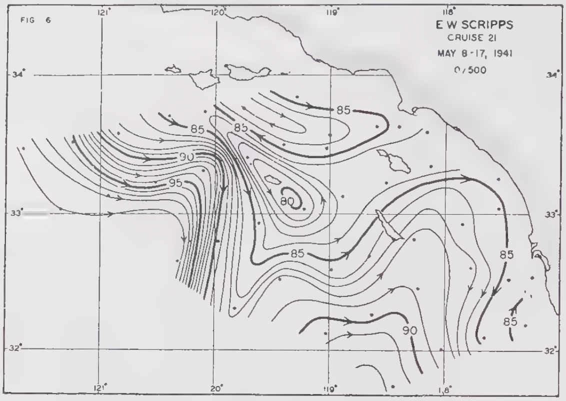

E W SCRIPPS
CRUISE 21
MAY 8-17, 1941
0/500
121°
120°
119°
118°
34°
33°
32°
85
90
95
80

FIG 7

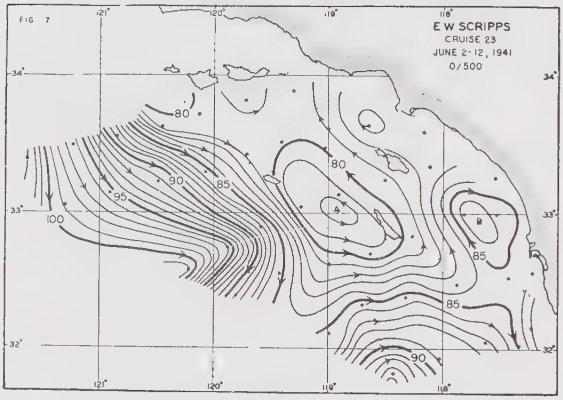
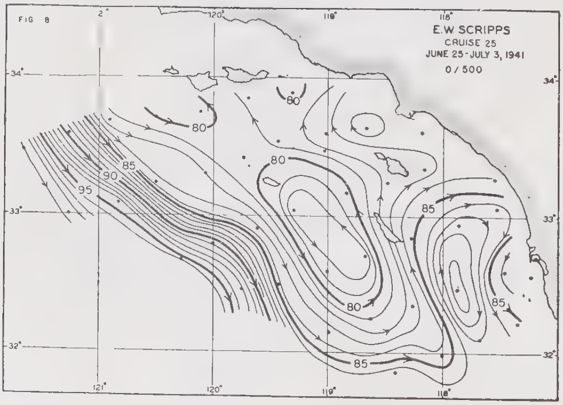

E W SCRIPPS
CRUISE 23
JUNE 2-12, 1941
0/500
121°
120°
119°
118°
34°
33°
32°
80
85
90
95
100

FIG 8


E.W SCRIPPS
CRUISE 25
JUNE 25-JULY 3, 1941
0/500
121°
120°
119°
118°
34°
33°
32°
80
85
90
95

Figures 6–8. Dynamic Height Anomalies (current boundaries) 0 over 500 Decibars, 1941.

level has the same general characteristics, but the position of maximum velocity shifts from 10 to nearly 30 kilometers at the last stage.

THE CONSERVATION OF ANGULAR MOMENTUM, AND RATE OF ENERGY DISSIPATION IN THE EQUIVALENT CIRCULAR EDDIES

The empirical curves drawn to show the relation of velocity to distance from the center of an eddy at its successive stages are only fair approximations to what might result from more detailed observations. Accordingly, only crude estimates of the quantities required can be obtained from these curves. Yet these curves must serve as a

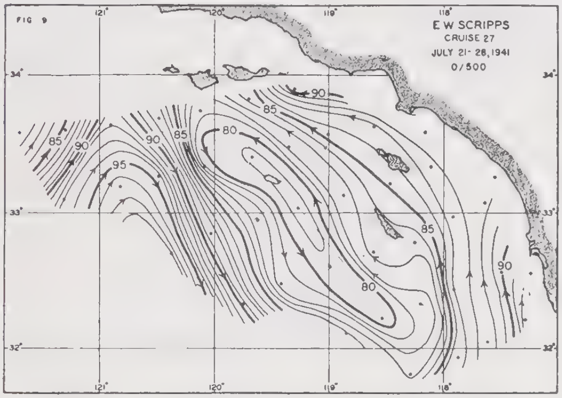


FIG 9
121°
120°
119°
118°
E W SCRIPPS
CRUISE 27
JULY 21-28,1941
0/500
34°
33°
32°
85
90
90
85
95
80
90
85
85
90
80

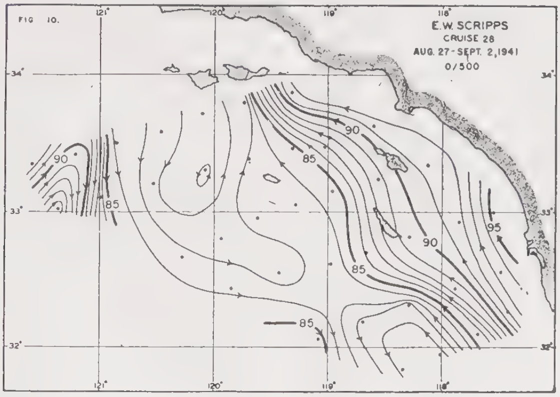


FIG 10.
121°
120°
119°
118°
E.W. SCRIPPS
CRUISE 28
AUG. 27-SEPT. 2,1941
0/500
34°
33°
32°
90
85
90
85
90
95
85
85

Figures 9, 10. Dynamic Height Anomalies (current boundaries) 0 over 500 Decibars, 1941.

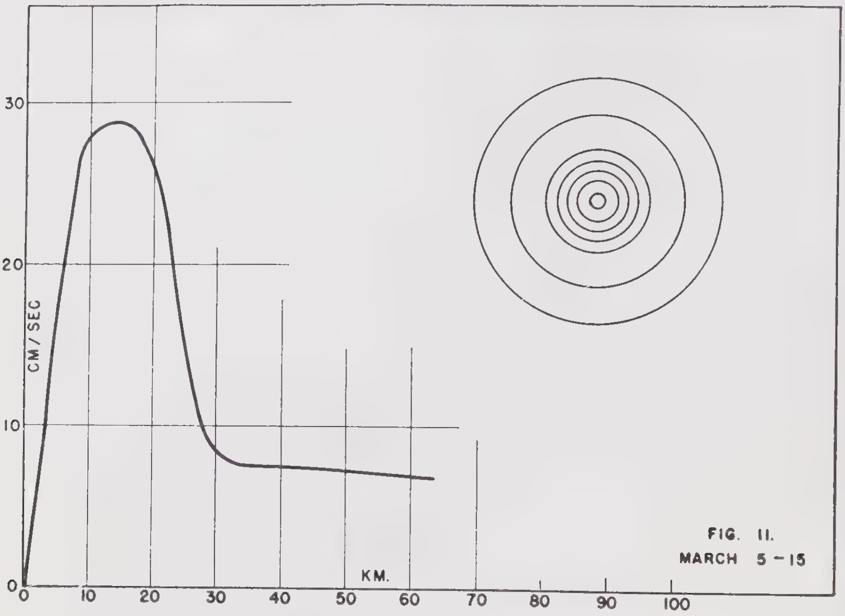


FIG. 11.
MARCH 5 – 15

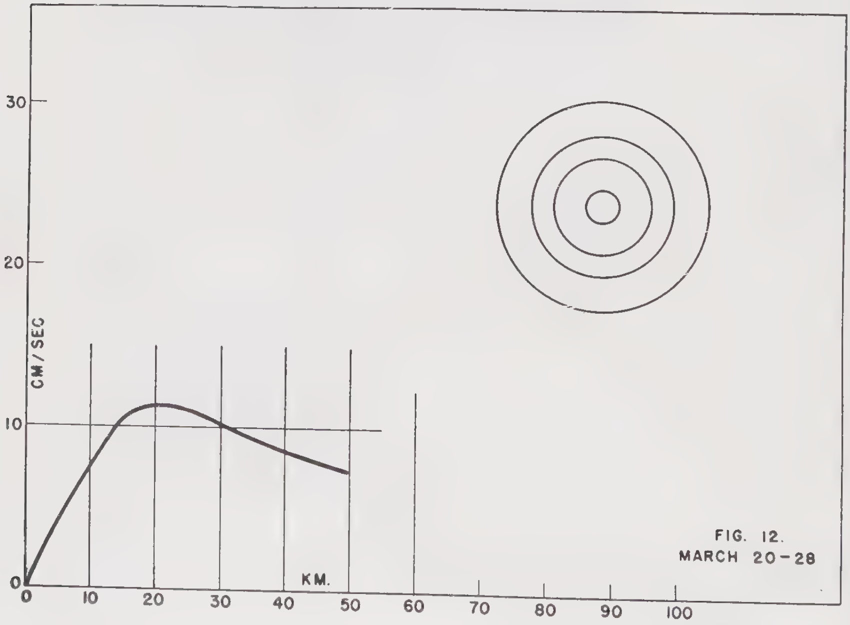


FIG. 12.
MARCH 20 – 28

Figures 11, 12. Circular models of eddies indicated on charts of Dynamic Height Anomalies, 0 over 500 Decibars, and relation of velocity to distance from center, 1940.

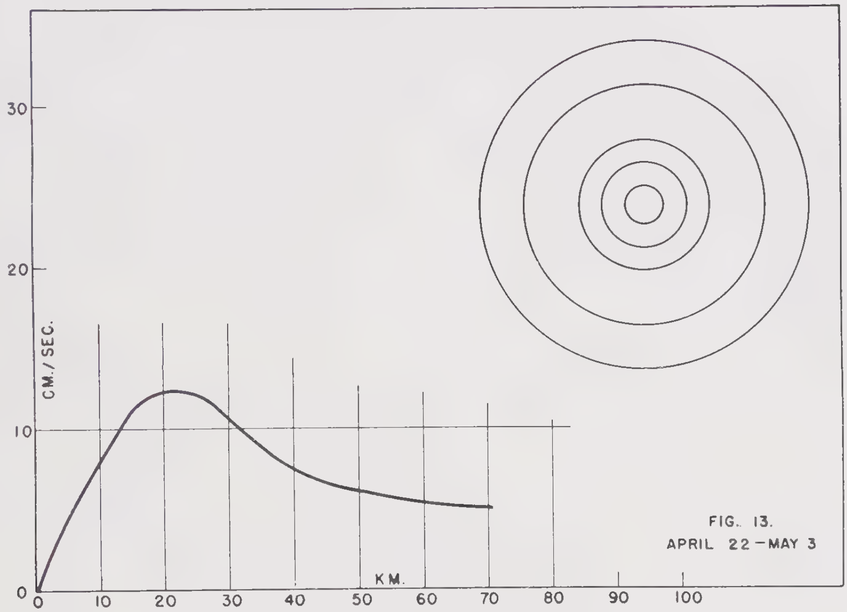


FIG. 13.
APRIL 22—MAY 3

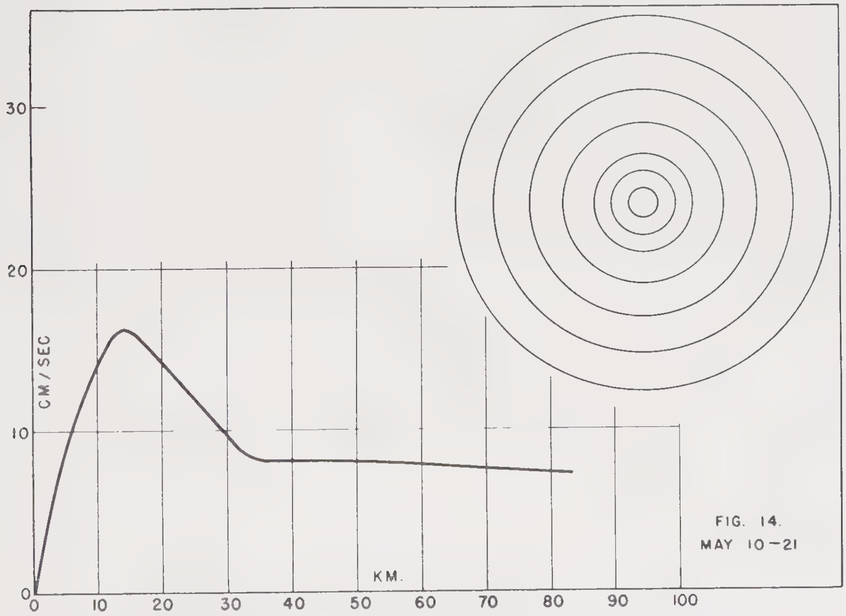


FIG. 14.
MAY 10—21

Figures 13, 14. Circular models of eddies indicated on charts of Dynamic Height Anomalies, 0 over 500 Decibars, and relation of velocity to distance from center, 1940.

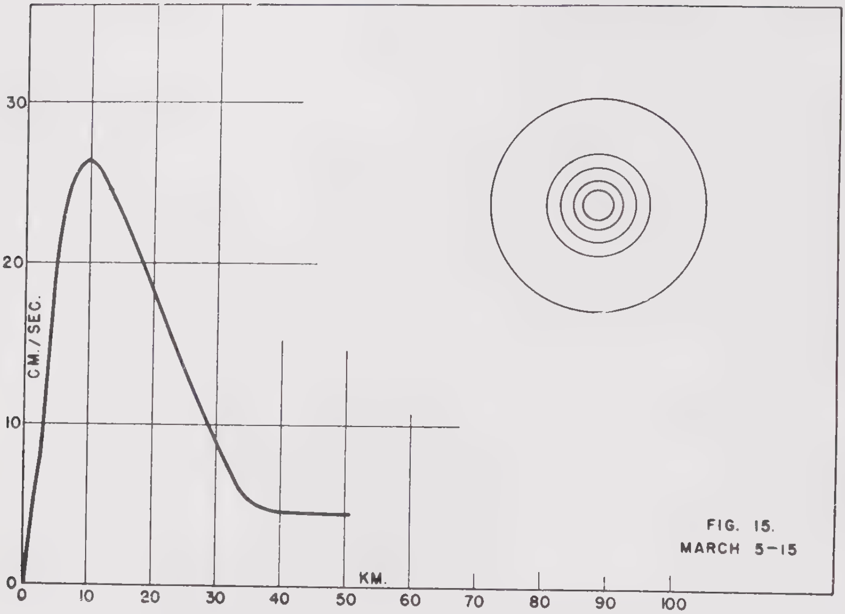


FIG. 15.
MARCH 5–15

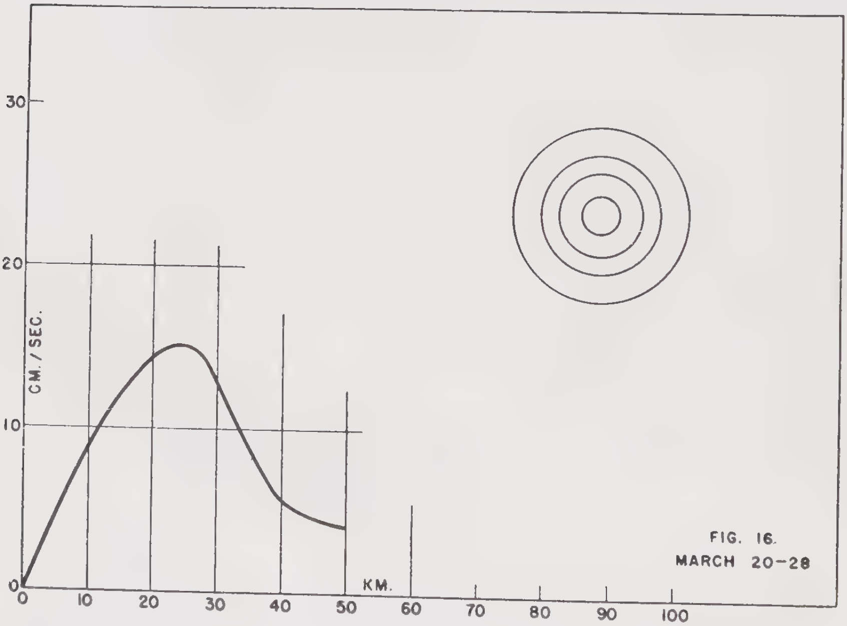


FIG. 16.
MARCH 20–28

Figures 15, 16. Circular models of eddies indicated on charts of Dynamic Height Anomalies, 50 over 500 Decibars, and relation of velocity to distance from center, 1940.

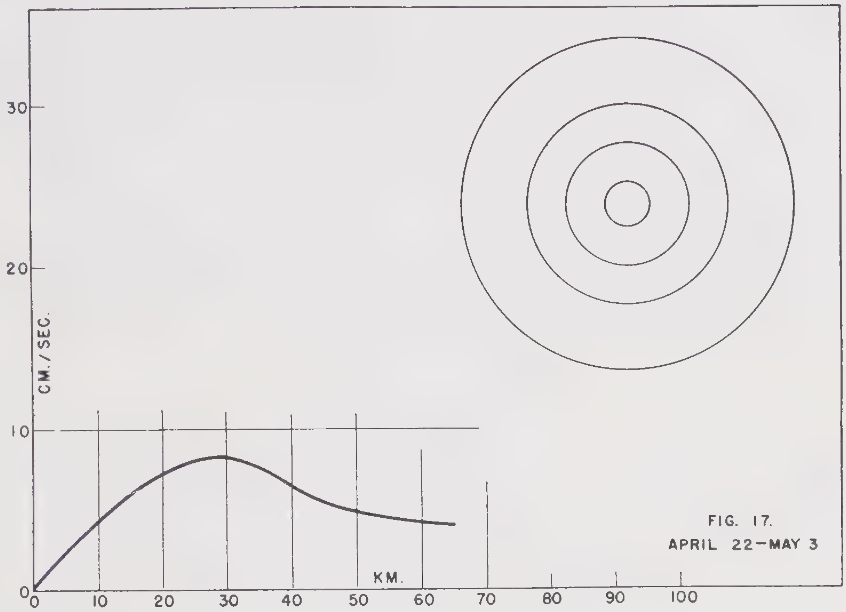


FIG. 17.
APRIL 22–MAY 3

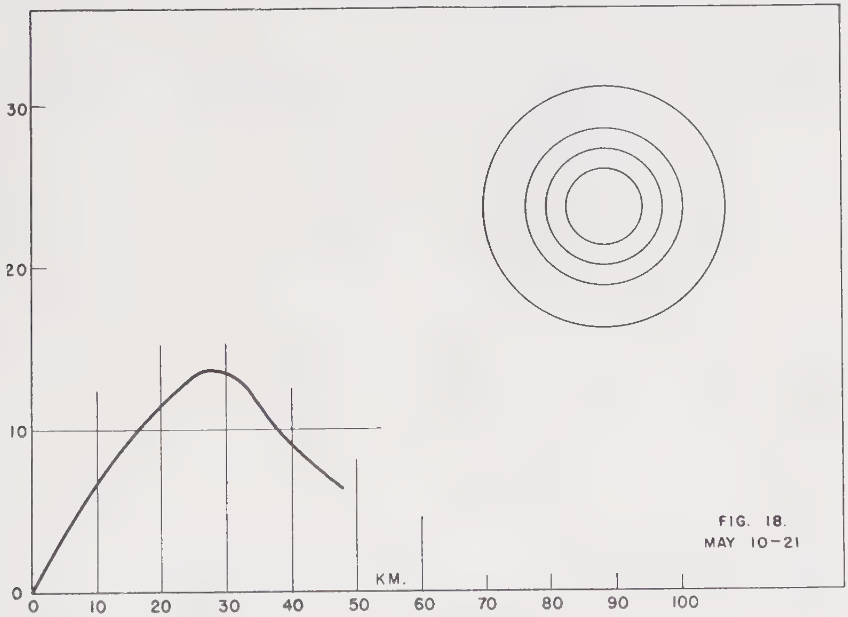


FIG. 18.
MAY 10–21

Figures 17, 18. Circular models of eddies indicated on charts of Dynamic Height Anomalies, 50 over 500 Decibars, and relation of velocity to distance from center, 1940.

basis for the first approach to the dynamics of the eddies, and by making several estimates of each quantity the errors may be reduced.

Since both the velocity and the velocity gradient decrease as the distance, r, from the center increases beyond that corresponding to the maximum velocity, external frictional forces may be neglected, if a sufficiently large portion of the eddy is used as a basis for computations.

Assuming only internal forces, the principle of the conservation of angular momentum applies to the eddy, considered as a mechanical system. Therefore, assuming unit density of the water, the angular momentum of unit thickness of the eddy,

$$\text{A. M.} = 2\pi \int_0^{r'} r^2 q dr \,, \tag{1}$$

should be constant at successive times, where q equals the velocity at distance r. A reasonable length of the maximum radius, r', of the eddies was determined by inspection of the charts and graphs to be 50 kilometers. If the same length is used for the successive stages of each series, a rough approximation will serve the purpose. Values of the angular momentum in c. g. s. units, computed by numerical integration of r^2q read from the empirical curves, are compiled in Table I.

TABLE I. Angular Momentum, in c. g. s. Units, of Horizontal Eddies at the Surface and at 50-meter Levels

1940	*0/500*	*50/500*	*Sum*
A	3.16×10^{21}	1.81×10^{21}	4.97×10^{21}
14 days			
B	2.46×10^{21}	2.14×10^{21}	4.60×10^{21}
34 days			
C	2.29×10^{21}	1.81×10^{21}	4.10×10^{21}
18 days			
D	2.76×10^{21}	2.24×10^{21}	5.00×10^{21}
1941	*0/500*		
A	4.85×10^{21}		
48 days			
B	4.81×10^{21}		
62 days			
C	2.47×10^{21}		

Considering the rather crude approximation of the empirical graph of q against r, the tabulated results agree well with the principle of the conservation of angular momentum.

Values of the kinetic energy, in c. g. s. units, computed for the same eddies by means of the formula

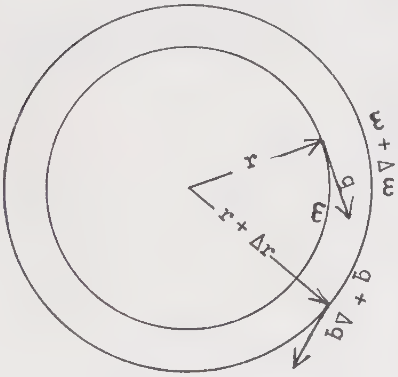
$$\text{K. E.} = 2\pi \int_{0}^{r'} r \left(\frac{q^2}{2}\right) dr\,, \tag{2}$$

are compiled in Table II.

TABLE II. Kinetic Energy, in c. g. s. Units, of Horizontal Eddies at the Surface and at 50-Meter Levels

1940	*0/500*	*50/500*	*Sum*
A	8.7×10^{15}	4.9×10^{15}	13.6×10^{15}
B	3.5×10^{15}	4.5×10^{15}	8.0×10^{15}
C	3.7×10^{15}	1.8×10^{15}	5.5×10^{15}
D	5.5×10^{15}	3.5×10^{15}	9.0×10^{15}
1941	*0/500*		
A	7.63×10^{15}		
B	6.57×10^{15}		
C	1.62×10^{15}		

Although the results are somewhat irregular, as was to be expected, there is a general decrease of the kinetic energy in the successive stages of each eddy, and estimates of the average rate of energy dissipation corresponding to various time intervals can easily be computed. The rates of loss of energy can also be computed from formulae involving velocity gradients and the coefficient of eddy viscosity a^2. If the motion is along parallel straight lines, the rate of energy dissipation per unit volume due to friction (Dryden, Murnaghan and Bateman, 1932: 157; Kalinske, 1939: 1394; 1940: 1236) can easily be shown to have the value $a^2\left(\frac{du}{dy}\right)^2$, where u equals the velocity in a direction perpendicular to y. The corresponding expression for motion in concentric circles, assuming circular symmetry of the velocity field, may be derived as follows: Referring to the diagram, where ω equals the angular velocity in radians per second,



$$(\omega + \Delta\omega)\,(r + \Delta r) = \omega r + \omega\Delta r + r\Delta\omega + [(\Delta\omega)\,(\Delta r)] = q_{r+\Delta r}\,,$$

$$\omega r = q_r\,,$$

and $$q_{r+\Delta r} - q_r = \omega\Delta r + r\Delta\omega + [(\Delta\omega)\,(\Delta r)]\,.$$

Therefore,

$$\frac{dq}{dr} = \omega + r\frac{d\omega}{dr} \text{ and } r\frac{d\omega}{dr} = \frac{dq}{dr} - \omega = \frac{dq}{dr} - \frac{q}{r}\,. \tag{3}$$

Since $r\Delta\omega$ equals that part of the velocity in the larger circle relative to that in the smaller circle, due to the change in angular velocity with reference to r, the frictional stress due to the relative velocity,

$$\left(r\frac{d\omega}{dr}\right)\Delta r = r\Delta\omega\,,$$

is

$$\frac{a^2\left(r\dfrac{d\omega}{dr}\right)\Delta r}{\Delta r}\,.$$

Therefore, the power loss per unit horizontal surface area is

$$\left[\frac{a^2\left(r\dfrac{d\omega}{dr}\right)\Delta r}{\Delta r}\right]\left[r\frac{d\omega}{dr}\Delta r\right].$$

Dividing this product by Δr gives the rate of dissipation of energy per unit volume, which reduces to

$$a^2\left(r\frac{d\omega}{dr}\right)^2 = a^2\left(\frac{dq}{dr} - \frac{q}{r}\right)^2.$$

Therefore, the rate of energy dissipation of an eddy of unit thickness is

$$2\pi a^2\int_0^{r'} r\left(\frac{dq}{dr} - \frac{q}{r}\right)^2 dr\,, \tag{4}$$

which can be found by numerical integration of the integrand, whose value can be estimated from the empirical graphs of q against r. Finally, by equating the two expressions for the average rates of energy loss,

$$2\pi a^2\int_0^{r'} r\left(\frac{dq}{dr} - \frac{q}{r}\right)^2 dr\Bigg]_{t_0,\,t_1}$$

$$= 2\pi \frac{\left. \int_0^{r'} r\left(\frac{q^2}{2}\right) dr \right]_{t_1} - \left. \int_0^{r'} r\left(\frac{q^2}{2}\right) dr \right]_{t_0}}{(t_1 - t_0)}, \qquad (5)$$

we obtain a formula for computing the coefficient of eddy viscosity,

$$a^2 = \frac{\left\{ \left[\int_0^{r'} r\left(\frac{q^2}{2}\right) dr \right]_{t_1} - \left. \int_0^{r'} r\left(\frac{q^2}{2}\right) dr \right]_{t_0} \right\}}{(t_1 - t_0) \left. \int_0^{r'} r\left(\frac{dq}{dr} - \frac{q}{r}\right)^2 dr \right]_{0 t_1}}, \qquad (6)$$

where the integral in the denominator should be averaged over the interval t_1 to t_0. A sufficiently close approximation for the present purpose is the arithmetic mean of the values of the integral corresponding to the times t_0 and t_1. The values of a^2 thus found from various combinations of kinetic energy values in Table II are presented in Table III.

TABLE III. VARIOUS ESTIMATES OF THE COEFFICIENT OF EDDY VISCOSITY a^2 IN C. G. S. UNITS

1940	*0/500*	*50/500*
A, B	4.9×10^5	0.3×10^5
A, C	1.8×10^5	1.3×10^5
A, D	0.8×10^5	0.4×10^5
A, E	1.9×10^5	1.3×10^5
1941	*0/500*	
A, B	0.7×10^5	
A, C	2.5×10^5	
B, C	5.7×10^5	

The range is rather large for each of the three series due to the crude empirical relation between q and r. Adopted median values of a^2 for later use are listed in Table IV.

TABLE IV. SELECTED MEDIAN VALUES OF THE COEFFICIENT OF EDDY VISCOSITY FOR EACH OF THREE SERIES OF EDDIES

Year	*Depths*	a^2
1940	0/500	1.5×10^5
1940	50/500	1.0×10^5
1941	0/500	3.0×10^5

PRELIMINARY STUDY OF LARGE EDDIES BASED ON VORTEX-FILAMENT THEORY

The foregoing evidence presented in support of the thesis appears to justify an attempt to predict, from the observed velocity distribution at the earliest date in each series, the relation of velocity to the distance from the center at the successive times of later surveys. This hydrodynamical problem will now be considered in the light of the resemblance of the observed velocity distribution in an eddy to the velocity distribution around a vortex-filament. For a detailed treatment of the vortex-filament, see Lamb (1945: 202–249), Prandtl (1935: 68), and Dryden, Murnaghan and Batemen (1932: 212–218). Vortex lines have the direction of the instantaneous axis of rotation of the fluid. A vortex-tube is formed by the collection of vortex lines perpendicular to a small closed curve, and the fluid within such a tube constitutes a vortex-filament. The circulation, Γ, of a closed curve is defined as the line integral of the tangential component of the velocity around the curve. Twice the angular velocity of the fluid elements is called the vorticity, and the product of the vorticity by the cross section of a vortex-filament equals the circulation which is constant for all cross sections of the tube. In this paper the vorticity will be denoted by ζ, corresponding to the vertical direction of the axis.

There is an instructive analogy between the dissolution of a vortex-filament generated in a viscous fluid and the conduction of heat from a small heated portion of a flat plate. The constant circulation of the vortex corresponds to a constant quantity of heat initially concentrated at a point. This quantity of heat will spread outward from the point by conduction in accordance with the following function,

$$S = \frac{K}{t} \exp\,(-\,r^2/4\nu t)\,, \tag{7}$$

which is a well known solution of the following differential equation of heat conduction, assuming circular symmetry about the point of concentration:

$$\frac{\partial S}{\partial t} = \nu \left(\frac{\partial^2 S}{\partial r^2} + \frac{1}{r} \frac{\partial S}{\partial r} \right); \tag{8}$$

S = amount of heat per unit area;
ν = coefficient of heat conduction;
r = distance from center;
t = time;
K = a constant.

The total amount of heat, within a circle of radius r, equals

$$2\pi \int_0^r rSdr = 4\nu\pi K\,[1 - \exp\,(-\,r^2/4\nu t)]\,, \tag{9}$$

which approaches the constant $4\nu\pi K$ as $r \longrightarrow \infty$, for all values of t. The same limit is approached as $t \longrightarrow 0$, for all values of r.

Leaving the problem of heat conduction, consider the analogous one of vorticity,

$$\Gamma = 2\pi \int_0^r K/t \exp\,(-\,r^2/4a^2t)\;rdr = 2\pi \int_0^r \zeta rdr$$

$$= 4a^2\pi K\,[1 - \exp\,(-\,r^2/4a^2t)], \tag{10}$$

where a^2 equals the coefficient of viscosity.

As $r \longrightarrow \infty$, $\Gamma \longrightarrow$ the constant $4a^2\pi K = \Gamma_1$, the circulation of an infinitely large circle. Therefore,

$$\Gamma = \Gamma_1\,[1 - \exp\,(-\,r^2/4a^2t)]\,. \tag{11}$$

The velocity, q, equals the circulation divided by the circumference:

$$q = \frac{\Gamma_1}{2\pi r}\,[1 - \exp\,(-\,r^2/4a^2t)]\,. \tag{12}$$

As $(r^2/4a^2t) \longrightarrow \infty$, $q \longrightarrow q_1 = \dfrac{\Gamma_1}{2\pi r}$ equals the usual circulatory motion with a potential. For small radial distances,

$$q = \frac{\Gamma_1 r}{2\pi}\,\{1/4a^2t - 1/2(r/4a^2t)^2 + \ldots\}\,. \tag{13}$$

Since $\zeta = (K/t) \exp\,(-\,r^2/4a^2t)$ from the heat conduction analogy, the vorticity equals

$$\zeta = \frac{\Gamma_1}{4a^2\pi t} \exp\,(-\,r^2/4a^2t)\,. \tag{14}$$

Therefore, on the axis

$$\zeta = \zeta_1 = \frac{\Gamma_1}{4a^2\pi t}\,, \tag{15}$$

and for very small radii, the velocity equals

$$q = \frac{\Gamma_1 r}{2\pi\,(4a^2t)} = \frac{\zeta_1}{2}\,r = \frac{\zeta_1 r_1}{2}\,\theta, \text{ where } r = r_1\theta\,. \tag{16}$$

In general,

$$q = \frac{\Gamma_1}{2\pi r}\left[1 - \exp\left(-r^2/4a^2t\right)\right] = \frac{\zeta_1 r_1}{2}\left[\frac{1 - \exp\left(-\dfrac{\theta^2 r_1^2}{4a^2 t}\right)}{\theta}\right]. \tag{17}$$

Accordingly for $t > 0$, the velocity around a vortex-filament is proportional to the distance from the center for small values of r. As r increases, the velocity is inversely proportional to r. Thus the velocity increases from zero to a maximum at some small value of r, and then decreases, approaching zero, as r increases indefinitely. However, as $t \rightarrow 0$, $\zeta_1 \rightarrow \infty$, and the position of maximum velocity approaches the axis. Thus, there is a general qualitative agreement between the velocity distribution around the vortex-filament and that observed in the eddies in the ocean. However, the initial position of the maximum velocity on the axis and the concentration of a very great vorticity in a very small area together constitute insuperable objections to the use of a vortex-filament as a model for detailed quantitative application to a large eddy in the sea. Yet, the general results already found suggest that it would be worth while to attempt the application of the fundamental concept of the vortex-filament to the eddy problem in such a way as to avoid the foregoing objections.

VORTICITY DISTRIBUTION OVER A CIRCULAR AREA AS A SATISFACTORY MODEL OF A LARGE EDDY IN THE OCEAN

In order to take advantage of the fundamental physical properties of the vortex-filament, and to avoid the objections referred to in the foregoing section, assume an initial distribution of vorticity over a circular area of appropriate radius, r_1. Moreover, in this attempt to devise a model of an eddy in the ocean, it will be necessary to place the whole theory on a sound physical basis, defined by the following accepted general hydrodynamical equations of motion in the sea (Sverdrup, Johnson and Fleming, 1942: 433; Sverdrup, 1942: 93, 96). In a left-hand rectangular coordinate system with positive z-axis the general hydrodynamical equations of motion in the ocean for the northern hemisphere are:

$$\frac{\partial u}{\partial t} + u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} + w\frac{\partial u}{\partial z} = 2\Omega\,(\sin\phi)\,v - \alpha\frac{\partial p}{\partial x} + \alpha R_x\,, \tag{19}$$

$$\frac{\partial v}{\partial t} + u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} + w\frac{\partial v}{\partial z} = -\,2\Omega\,(\sin\phi)\,u - \alpha\frac{\partial p}{\partial y} + \alpha R_y\,, \tag{20}$$

$$\frac{\partial w}{\partial t} + u\frac{\partial w}{\partial x} + v\frac{\partial w}{\partial y} + w\frac{\partial w}{\partial z} = -\,2\Omega\,(\sin\phi)\,v_E + g - \alpha\frac{\partial p}{\partial z} + \alpha R_z\,. \qquad (21)$$

u, v, w,	the velocity components along the coordinate axes;
v_E	the horizontal velocity toward the east;
Ω,	angular velocity of earth's rotation = .729 x 10^{-3};
ϕ,	geographic latitude;
α,	specific volume of the water;
p,	pressure;
R_x, R_y, R_z,	components of the frictional force per unit volume;
g,	acceleration of gravity.

For the southern hemisphere, change the signs of the first terms on the right-hand side of the first two equations.

Consider only horizontal motion and assume small variations of latitude. Let $2\,\Omega\sin\phi$ = a constant average value, λ, and replace the symbols R, denoting fluid friction, by $a^2\nabla^2 u$, and $a^2\nabla^2 v$, thus obtaining the Navier-Stokes equations of motion in the sea (Sverdrup, Johnson and Fleming, 1942: 470):

$$\frac{\partial u}{\partial t} + u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} = -\,\alpha\frac{\partial p}{\partial x} + \lambda v + a^2\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right), \qquad (22)$$

$$\frac{\partial v}{\partial t} + u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} = -\,\alpha\frac{\partial p}{\partial y} - \lambda u + a^2\left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2}\right). \qquad (23)$$

(a^2 = kinematic coefficient of eddy viscosity, assumed to be constant.) Take the negative partial derivative of equation (22) with respect to y and the positive partial derivative of equation (23) with respect to x, and add the results:

$$\frac{\partial}{\partial t}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right) + u\frac{\partial}{\partial x}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right) + v\frac{\partial}{\partial y}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right) + \frac{\partial u}{\partial x}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right)$$
$$+ \frac{\partial v}{\partial x}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right) = a^2\left[\frac{\partial}{\partial x^2}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right) + \frac{\partial}{\partial y^2}\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right)\right]. \qquad (24)$$

Substitute ζ for the vorticity, $\left(\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}\right)$ = curl of the velocity (Lamb, 1945: 202), and assume the equation of continuity,

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} = 0\,,$$

thus obtaining

$$\frac{\partial \zeta}{\partial t} = a^2\left(\frac{\partial^2 \zeta}{\partial x^2} + \frac{\partial^2 \zeta}{\partial y^2}\right) - \left(u\frac{\partial \zeta}{\partial x} + v\frac{\partial \zeta}{\partial y}\right). \qquad (25)$$

Equations for transforming from rectangular to polar coordinates, assuming circular symmetry or $\partial/\partial\theta$ and $\partial^2/\partial\theta^2 = 0$ (Gibson, 1931: 113–115; Woods, 1926: 72–73), are

$$\frac{\partial f}{\partial x} = \frac{\partial f}{\partial r}\cos\theta\,, \quad \frac{\partial f}{\partial y} = \frac{\partial f}{\partial r}\sin\theta\,, \quad \frac{\partial^2 f}{\partial x^2} = \frac{\partial^2 f}{\partial r^2}\cos^2\theta + \frac{\partial f}{\partial r}\frac{\sin^2\theta}{\mathrm{r}}\,,$$

$$\frac{\partial^2 f}{\partial y^2} = \frac{\partial^2 f}{\partial r^2}\sin^2\theta + \frac{\partial f}{\partial r}\frac{\cos^2\theta}{r}\,, \quad \frac{\partial^2 f}{\partial x \partial y} = \frac{\sin 2\theta}{2}\left(\frac{\partial^2 f}{\partial r^2} - \frac{1}{r}\frac{\partial f}{\partial r}\right).$$

For circular symmetry,

$$\left(u\frac{\partial\zeta}{\partial x} + v\frac{\partial\zeta}{\partial y}\right)$$

reduces to

$$u\frac{\partial\zeta}{\partial r}\cos\theta + v\frac{\partial\zeta}{\partial r}\sin\theta = -\,q\frac{\partial\zeta}{\partial r}(\sin\theta\cos\theta - \cos\theta\sin\theta) = 0\,,$$

since $u = -\,q\sin\theta$ and $v = q\cos\theta$.
Therefore, the final equation is

$$\frac{\partial\zeta}{\partial t} = a^2\left(\frac{\partial^2\zeta}{\partial x^2} + \frac{\partial^2\zeta}{\partial y^2}\right). \tag{26}$$

For circular symmetry

$$\frac{\partial^2\zeta}{\partial x^2} = \frac{\partial^2\zeta}{\partial r^2}\left(\frac{x^2}{x^2+y^2}\right) + \frac{\partial\zeta}{\partial r}\frac{y^2}{(x^2+y^2)\sqrt{x^2+y^2}}\,,$$

$$\frac{\partial^2\zeta}{\partial y^2} = \frac{\partial^2\zeta}{\partial r^2}\left(\frac{y^2}{x^2+y^2}\right) + \frac{\partial\zeta}{\partial r}\frac{x^2}{(x^2+y^2)\sqrt{x^2+y^2}}\,.$$

Substituting these expressions and simplifying gives the equation of diffusion of vorticity in the sea,

$$\frac{\partial\zeta}{\partial t} = a^2\left(\frac{\partial^2\zeta}{\partial r^2} + \frac{1}{r}\frac{\partial\zeta}{\partial r}\right), \tag{27}$$

which is the same form as the equation of heat conduction (8). Thus the analogy of vorticity diffusion to heat conduction used in the section on the vortex-filament is established for motion in the sea.

If the coefficient of eddy viscosity is not restricted to the constant value a^2, but is assumed to be μ, a function of x and y, a method similar to the foregoing yields the equation

$$\frac{\partial\zeta}{\partial t} = \mu\left(\frac{\partial^2\zeta}{\partial r^2} + \frac{1}{r}\frac{\partial\zeta}{\partial r}\right) + \zeta\left(\frac{\partial^2\mu}{\partial r^2} + \frac{1}{r}\frac{\partial\mu}{\partial r}\right) + 2\frac{\partial\mu}{\partial r}\frac{\partial\zeta}{\partial r}\,, \tag{28}$$

where μ is a function of r.

Having derived equation (27) of the diffusion of vorticity in the sea, consider initial conditions adapted to a large eddy:

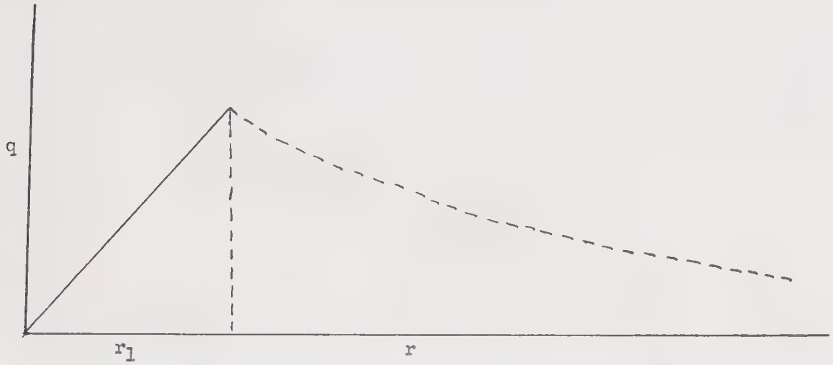
$$\zeta = \zeta_1\,, \quad r \leqq r_1\,, \quad t = 0\,,$$
$$\zeta = 0\,, \quad r > r_1\,, \quad t = 0\,,$$

where ζ_1 is constant and r_1 is a constant radius to be determined. Then the initial velocity distribution is given by equations

$$q = \frac{\zeta_1 \int_0^r 2\pi r dr}{2\pi r} = \frac{\zeta_1 r}{2} = \left(\frac{\zeta_1 r_1}{2}\right)\theta\,, \quad \theta = r/r_1 \leqq 1\,, \tag{29}$$

$$q = \frac{\zeta_1 \int_0^\infty 2\pi r dr}{2\pi r} = \frac{\zeta_1 \int_0^{r_1} 2\pi r dr}{2\pi r} = \frac{\zeta_1 r_1^2}{2r} = \left(\frac{\zeta_1 r_1}{2}\right)\frac{1}{\theta}\,, \quad \theta > 1\,. \tag{30}$$

In such a model the initial velocity would be proportional to r for $r \leqq r_1$ and inversely to r for $r > r_1$, with a maximum value $\frac{\zeta_1 r_1}{2}$ at the distance r_1, as shown in the following diagram:



The graphs (Figs. 11 and 16), corresponding to the earliest dates of the 1940 surveys, may be regarded as in good agreement with the slight alteration of this diagram, expected to represent the effect of diffusion during the time from the initial conditions to that of the first cruise of the series.

We shall now attempt to find a solution of equation (27) that satisfies the foregoing initial conditions. A well known elementary solution is

$$F(\lambda)\exp(-\lambda^2 a^2 t)\, J_0(\lambda r)\,,$$

where $F(\lambda)$ is an arbitrary function of λ and J_0 is a Bessel function of zero order. Summing these elementary solutions with respect to λ, which is independent of t and r, gives the formal solution

$$\zeta = \int_0^\infty F(\lambda)\, J_0\,(\lambda r) \exp\,(-\,\lambda^2 a^2 t)\, d\lambda\,. \tag{31}$$

For $t = 0$, we require that

$$\int_0^\infty F(\lambda)\, J_0\,(\lambda r)\, d\lambda = \begin{cases} \zeta_1\,, & r \lesseqgtr r_1 \\ 0\,, & r > r_1 \end{cases}. \tag{32}$$

According to Gray, Mathews and MacRobert (1922: 64–78)

$$\int_0^\infty J_1\,(x)\, J_0\,(\alpha x)\, dx = \begin{cases} 1\,, & \alpha^2 < 1 \\ 1/2\,, & \alpha^2 = 1 \\ 0\,, & \alpha^2 > 1 \end{cases}. \tag{33}$$

Therefore, we readily obtain the required formal solution

$$\zeta = \zeta_1\, r_1 \int_0^\infty J_1\,(\lambda r_1)\, J_0\,(\lambda r) \exp\,(-\,\lambda^2 a^2 t)\, d\lambda\,. \tag{34}$$

This is mathematically the same solution as that investigated by McEwen (1946: 618) in a problem of diffusion of heat or particulate matter from a circular area of concentration. Accordingly, the same transformations of the formal equation to expressions adapted to numerical work will be restated here:

$$\zeta = \zeta_1\,[1 - \exp\,(-\,r_1^2/4a^2t)]\,,\ \text{for } r = 0\,, \tag{35}$$

$$\zeta = (\zeta_1/2)\,[1 - I_0\,(r_1^2/2a^2t) \exp\,(-\,r_1^2/2a^2t)]\,,\ \text{for } r = r_1, \tag{36}$$

$$\zeta = \zeta_1\,\{[1 - \exp\,(-\,r_1^2/4a^2t)] - (r_1/2a^2t) \exp\,(-\,r_1^2/4a^2t) \int_0^r I_1\,(rr_1/2a^2t) \exp\,(-\,r^2/4a^2t)\, dr\}\,, \tag{37}$$

where $I_i\,(x)$ is the modified Bessel function of the first kind. Also, the function $e^{-x} I_i\,(x)$, denoted by $f_i\,(x)$, has been calculated for $i = 0$ to 23, $x = 0$ to 20; the results are available in photostat copies on file at the Scripps Institution. Accordingly, equation (36) reduces to

$$\zeta = (\zeta_1/2)\,[1 - f_0\,(r_1^2/2a^2t)]\,,\ \text{for } r = r_1\,. \tag{38}$$

Equation (37) can be evaluated by numerical integration. However, by repeated application of integration by parts, McEwen (1946: 618) obtained the expansion ζ into the convergent series

$$\zeta = \zeta_1 \left\{ 1 - e^{-\frac{(r-r_1)^2}{4a^2t}} \left[f_0\left(\frac{r\,r_1}{2a^2t}\right) + \left(\frac{r}{r_1}\right) f_1\left(\frac{r\,r_1}{2a^2t}\right) \right.\right.$$
$$\left.\left. + \left(\frac{r}{r_1}\right)^2 f_2\left(\frac{r\,r_1}{2a^2t}\right) + \ldots \right] \right\} \begin{matrix}\text{for}\\ r < r_1\end{matrix}\,, \qquad (39)$$

and

$$\zeta = \zeta_1\, e^{-\frac{(r-r_1)^2}{4a^2t}} \left\{ \frac{r_1}{r} f_1\left(\frac{r\,r_1}{2a^2t}\right) + \left(\frac{r_1}{r}\right)^2 f_2\left(\frac{r\,r_1}{2a^2t}\right) \right.$$
$$\left. + \left(\frac{r_1}{r}\right)^3 f_3\left(\frac{r\,r_1}{2a^2t}\right) + \ldots \right\} \begin{matrix}\text{for}\\ r > r_1\end{matrix}\,. \qquad (40)$$

Having thus obtained a series of values of ζ as a function of r corresponding to any value of t, the velocity q can be obtained from

$$q = \frac{\int_0^r \zeta r dr}{r} \qquad (41)$$

by numerical integration. The corresponding formal equation of velocity is

$$q = \zeta_1\, r_1 \int_0^\infty \frac{J_1\,(\lambda r_1)\; J_1\,(\lambda r)}{\lambda} \exp\,(-\,a^2t\lambda^2)\; d\lambda\,, \qquad (42)$$

which can be reduced to

$$q = \frac{\zeta_1 r_1}{2} \left\{ 1 - [f_0\,(r_1^2/2a^2t) + f_1\,(r_1^2/2a^2t)] \right\} \qquad (43)$$

for $r = r_1$. This equation, which can easily be evaluated from the manuscript tables of $f_0(x)$ and $f_1(x)$, serves as a useful check on the foregoing methods of computation.

For convenience in carrying out the computations corresponding to a series of values of t, required in applications to the observations, the formulae were transformed as follows, using the equation $r = r_1\theta$. Denoting by $\{\ \}_1$ the coefficient of ζ_1, equation (39), and by $\{\ \}_2$ the coefficient of ζ_1, equation (40),

$$q = \left(\frac{\zeta_1 r_1}{2}\right) \frac{\int_0^\theta 2\,\{\ \}_1\,\theta d\theta}{\theta}\,, \quad \theta \leqq 1\,, \qquad (44)$$

$$q = \frac{\int_0^1 2\,\{\ \}_1\,\theta d\theta + \int_1^\theta \{\ \}_2\,\theta d\theta}{\theta}\,, \quad \theta > 1\,. \tag{45}$$

For any value of t, $r_1^2/4a^2t$ = a constant c. Accordingly,

$$\{\ \}_1 = 1 - \exp\left(- c\,[1 - \theta]^2\right)\,[f_0(2c\theta) + \theta f_1\,(2c\theta) + \theta^2 f_2\,(2c\theta) + \ldots]\,, \tag{46}$$

$$\{\ \}_2 = 2 \exp\left(- c\,[1 - \theta]^2\right)\,[(1/\theta)\,f_1\,(2c\theta) + (1/\theta)^2 f_2\,(2c\theta) + (1/\theta)^3 f_3\,(2c\theta) + \ldots]\,. \tag{47}$$

The values of $\{\ \}_1$ and $\{\ \}_2$ can also be computed by means of the single equation (37), using the same transformation, thus:

$$\{[1 - e^{-c}] - 2c \int_0^\theta e^{-c(1-\theta)^2} f_1\,(2c\theta)\,d\theta\}\,, \tag{48}$$

which can be evaluated by numerical integration.

PREDICTION OF VELOCITIES IN CIRCULAR EDDIES BY MEANS OF THE FOREGOING MODEL, COMPARED WITH THOSE OBSERVED

Values of the vorticity, ζ, and the relative velocity, q', as functions of the distance, r, were computed by means of the foregoing formulae, corresponding to each of the three values of the coefficient of eddy-viscosity, a^2, found by the energy method, and for times, t, equal to 0, 1, 2, 3, . . . 15 days. The value t_0 of t, for which the computed relative velocities agreed best with the observed relative velocities at the earliest survey date of each of the three series of cruises, was found by comparing computed and observed graphs. This time, t_0, is the estimated time from the initial condition when $\zeta = \zeta_1$ for $r \overset{=}{<} r_1$ and $\zeta = 0$ for $r > r_1$, corresponding to the first cruise of the series. In all three cases, the value 6 was selected for t_0. The value of r_1 was found by inspection of the empirical curves of q plotted against r to be 10 kilometers for 1940 and 30 kilometers for 1941 (page 194). In each case a value was assigned to the constant coefficient $(\zeta_1 r_1/2)$ that showed the best agreement between the computed and observed velocities for $t = t_0$. As already shown on pages 207–209, this coefficient is the maximum velocity and corresponds to $r = r_1$ and $t = 0$. For the surface, and the 50-meter level, 1940, and the surface, 1941, these coefficients were found to have the respective values: 42, 35.3 and 18 cm/sec. It remains to determine the value of t corresponding to each cruise by adding to the first value, 6, the time from the first to the second cruise, from the second to the third, etc., and to evaluate the formulae for each value of t thus determined, in order to predict the velocity distributions. The three series of such theoretical results shown by the curves, Figs. 19–23, 24–28, and 29–33, are to be compared with the histograms representing corresponding average velocities observed between the indicated values of r. The general agreement between theory and observation appears to be sufficiently close to prove the thesis offered at the beginning.

CONCLUDING REMARKS

Consideration of the problem of large eddies as a whole leads to calling attention to certain points not specifically mentioned before.

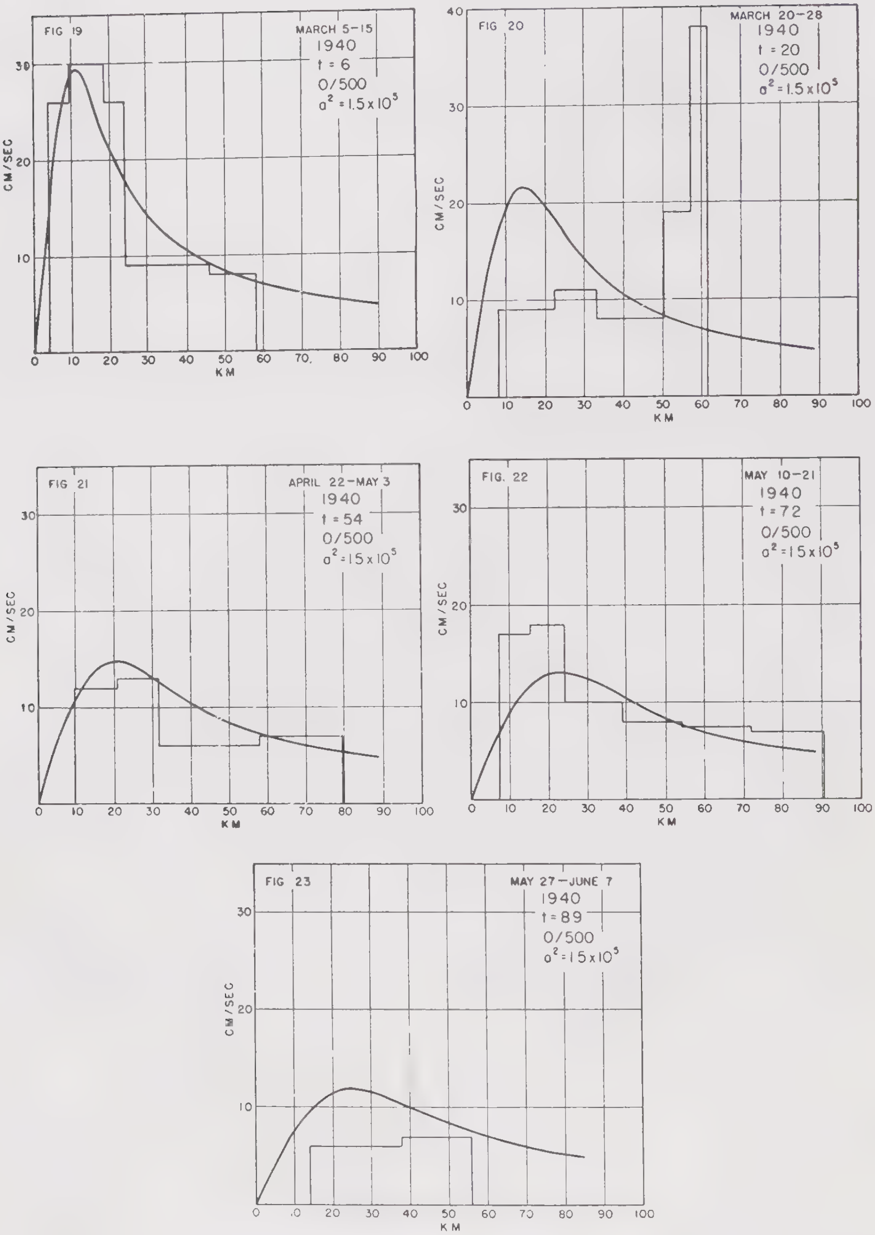
First, the basic hydrodynamic equations (page 204) contained no term representing the wind stress. This omission is justified because the eddies were shown to agree with the principle of the conservation of angular momentum, thus implying that the resultant torque of the wind stress was zero.

Second, the equation of vorticity implies that the shearing stress is due to the horizontal transport of available initial vorticity. This conservative property of vorticity also implies no solenoids in the horizontal plane, no vertical velocity or a uniform distribution of vertical velocity, and no horizontal convergence or divergence (Petterssen and Austin, 1942: 17–19).

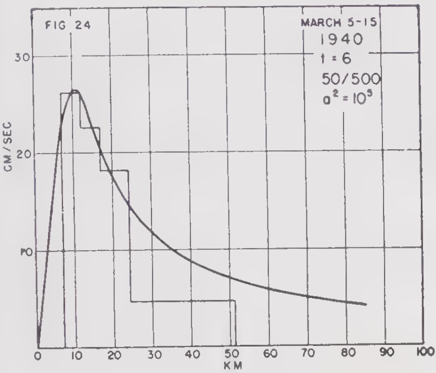
Third, in a circular vortex the fluid elements or particles move in circular orbits around a common axis and all particles lying on one and the same circle have one and the same velocity. In the limiting case of steady motion, the circles around the axis are likewise the paths of the particles and the lines of flow represent the field of velocity (Bjerknes, 1921: 31).

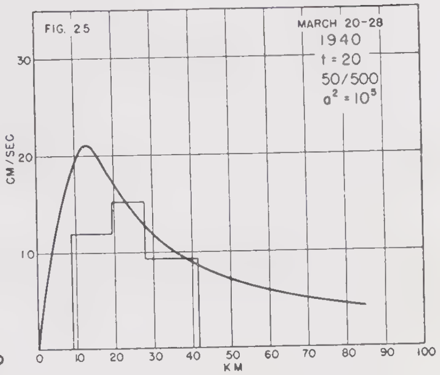
Fourth, it follows from equation (41) that $\frac{q}{r} + \frac{dq}{dr} = \zeta$. From this, the integrand in equation (4) of the rate of dissipation of kinetic energy can be expressed in the form $r\,(\zeta - 2\,q/r)^2$, which is a convenient expression for direct numerical tabulation, in using the theoretical relation of q to r.

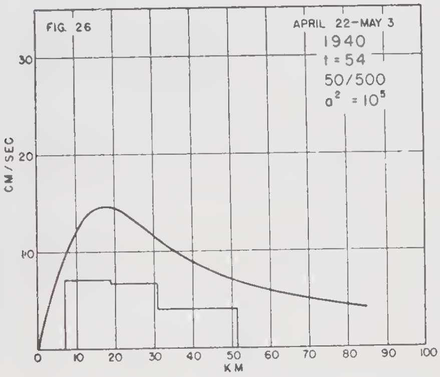
In attempting to apply mathematics to the investigation of any real phenomena, it is necessary to devise a simplified model of the phenomena. In such a model, actual conditions are necessarily simplified and various details are ignored. The success of this kind of an attack depends upon the extent to which essential features of the actual phenomena are preserved, and upon the relative importance of the details ignored. If any elements of the mathematical model depart essen-

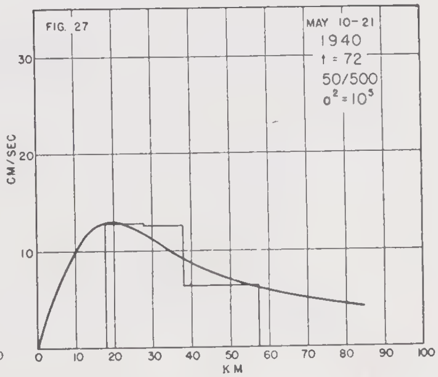


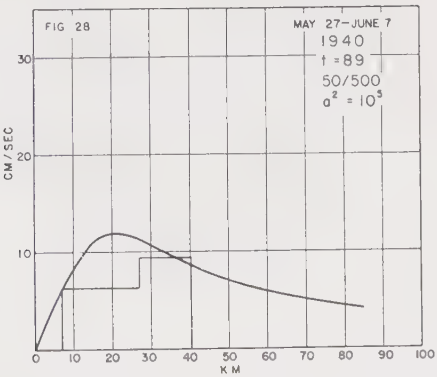
Figures 19–23. Curves of theoretical relation of velocity to distance from center of eddies, and histograms of velocity corresponding to average distance between lines of Dynamic Anomaly curves (current boundary lines). 0 over 500 Decibars. 1940.



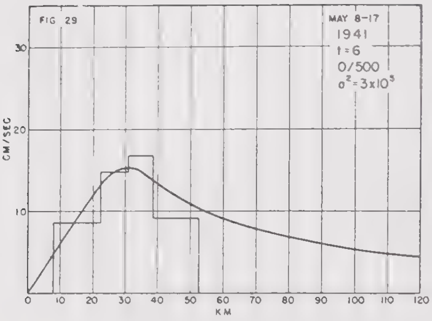


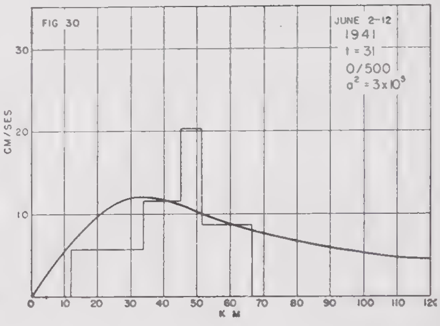


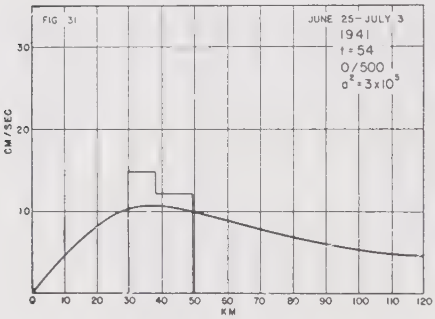


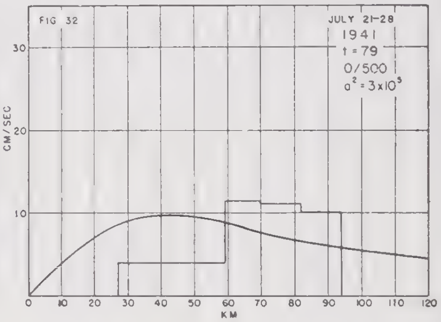


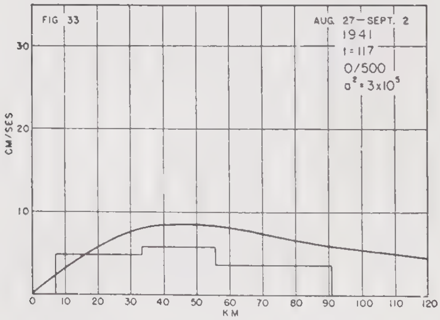
Figures 24–28. Curves of theoretical relation of velocity to distance from center of eddies, and histograms of velocity corresponding to average distance between lines of Dynamic Anomaly curves (current boundary lines), 50 over 500 Decibars, 1940.











Figures 29–33. Curves of theoretical relation of velocity to distance from center of eddies, and histograms of velocity corresponding to average distance between lines of Dynamic Anomaly curves (current boundary lines), 0 over 500 Decibars, 1941.

tially from the reality, the deductions from it may seriously contradict the observations. Since we can not be sure beforehand regarding the adequacy of any model that we may devise, we must test it by making deductions from it and comparing them with observations. Thus, by a trial and error method we may eventually succeed in devising a model sufficiently in accord with reality, yet simple enough to deal with mathematically.

It follows from consideration of the various observed features of the large eddies, and the corresponding deduced results, that, taken as a whole, the evidence is convincing in support of the initialthes is regarding large horizontal eddies in the sea off southern California.

Also, it may be mentioned that, assuming an appropriate initial constant low temperature of a circular area of a 60-kilometer radius, centered at the center of the surface eddy in 1940, the average temperature varied with distance from the center, as would be expected from the law of lateral diffusion. The surface salinity in 1941 also conformed to the same diffusion equation. The coefficients of diffusion obtained in this way were respectively, 1.8×10^7 and $.54 \times 10^7$ c. g. s., which are in good agreement with values for this region found by other methods (Sverdrup, Johnson and Fleming, 1942: 485). These general conclusions imply that the water mass maintains its integrity and position.

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Contribution No. 384

STREAMLINES FROM A DISCRETE VECTOR FIELD: WITH APPLICATION TO OCEAN CURRENTS[1]

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INTRODUCTION

The problem of presenting a scalar field on the surface of the earth or sea can be solved by drawing the contour lines or isopleths of the field. If the values of the scalar are measured at points of a grid, it is necessary to interpolate between the points in constructing the contours. The resulting curves are therefore somewhat subjective; however, if the data are reasonably accurate and closely spaced, experienced workers can reduce this subjectiveness to a minimum.

The cartographic problem of representing a vector field, such as of surface currents or of winds, can be solved by drawing the streamlines. The art of interpolating between grid points and of drawing the streamlines is considerably more difficult than that of constructing the isopleths of a scalar field. The subjective element is stronger, especially when the data are widely spread and only moderately accurate. If the streamline problem could be reduced to one of contouring a scalar field, then much of the subjective nature of the problem would be removed. Also inherent in this problem is the necessity of developing an objective method of smoothing the data to reduce the effect of random observational errors.

In this paper a method is derived whereby the problem of drawing streamlines is reduced to one of contouring a scalar distribution; this method applies to the special case of an ocean without horizontal divergence. An indication of the method of attacking the more general case is given towards the end of the paper. The application of the special solution to the real ocean is discussed, and an example

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[2] Now with the Oceanographic Studies Branch, United States Navy Electronics Laboratory, San Diego, California.

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is given. The scalar quantity to be contoured in the special case of horizontal nondivergent flow is called the stream function. In contouring the stream function one has an advantage not encountered in contouring the usual scalar field, for the isopleths, or streamlines, should be parallel to the velocity vectors; and hence, besides using the numerical values of the stream function, certain details of the streamlines may be brought out by using the vectors themselves as directional guides. The contours of the stream function, however, give the general flow pattern which is frequently lost when only the directional qualities of the vectors are used directly.

STREAMLINES FOR A TWO-DIMENSIONAL NONDIVERGENT VELOCITY FIELD

In this special case the streamlines are contours of the so-called stream function. In the following discussion, consider a velocity vector field, with the vectors given at the points of a grid. The x and y components of the velocity are $u(x, y)$ and $v(x, y)$ respectively. With this notation, it can be shown (see Sokolnikoff, *et al.*, 1941: 221) that the stream function $\Psi(x, y)$ is related to the velocity field by

$$(1) \qquad \frac{\partial \Psi}{\partial x} = - v\,, \qquad \frac{\partial \Psi}{\partial y} = + u\,.$$

Solving these equations for the stream function,

$$(2) \qquad \Psi\,(x, y) = \int_{a,\,b}^{x,\,y} (- v dx + u dy)\,.$$

The problem of finding the scalar function, the contours of which are streamlines, is thus reduced to the problem of numerical integration of equation (2). Consider the grid of velocity vectors described above to extend to n in the x-direction and to m in the y-direction. For every point in the field defined by an integer combination of the coordinates x and y, there exists a value of u and of v. Let $u_{i,j}$ and $v_{i,j}$ be the values of the components found at the intersection of the i^{th} column and the j^{th} row. For the purposes of the numerical integration, the following sums are introduced:

$$(3) \quad \text{(a)}\ (\psi_y)_{l,\,j+1/2} = \sum_{j=0}^{k} u_{l,\,j}\Delta y \qquad \text{(For each } l,\ k \text{ takes on successive values from 1 to } m\text{)}$$

$$\text{(b)}\ (\psi_x)_{i+1/2,\,k} = -\sum_{i=0} v_{i,\,k}\Delta x \qquad \text{(For each } k,\ l \text{ takes on successive values from 1 to } n\text{).}$$

Equation (3a) signifies the summation of u along a particular (l) value of x. For each particular value of l, k takes on successive values from 1 to m. Hence, for each value of l there are m equations of the form (3a), each one giving a value of ψ_y. There are n columns along which these partial summations are performed; that is, l takes on successive values from 1 to n. Hence, there are as many values of ψ_y as there are grid points. These values are assumed to apply along the grid lines parallel to the y-axis, and at points midway between the grid points. Similarly, equation (3b) signifies the summation of v along a particular (k) value of y, and for each of these values of k, l takes on successive values from 1 to n. The resulting mn values of ψ_x are assumed to apply along the grid lines parallel to the x-axis, and at points midway between the grid points. ψ_x equals zero along the line $x = \frac{1}{2}$, and ψ_y equals zero along the line $y = \frac{1}{2}$.

The discrete values of ψ_x and ψ_y thus found may be thought of as representing numerical values of a series of continuous functions, one such function of ψ_y applying for each of the columns of the grid, and one such function of ψ_x applying for each of the rows of the grid. These functions represent a sort of "line" stream function, applicable only for the particular velocity component summed, and for the line along which the summation is performed. We have at this point two fields of "line" stream functions; the numerical differentiation of one of these fields in the y-direction yields the x component of the velocity, and the numerical differentiation of the other field in the x-direction yields the y component of the velocity.

It is desired, however, to obtain *one* set of numbers in the field which represents one stream function, the differentiation of which in any particular direction yields the velocity component normal to that direction. Assume for the moment that the vector field being investigated is a true nondivergent field. In this case any particular row of values of ψ_x or column of values of ψ_y differs from the true values of the stream function along that particular row or column only by a constant of integration. This constant is different for each row and column. It is thus necessary to find the set of constants to be added to the rows of ψ_x's and to the columns of ψ_y's in order to make the two fields coincide.

Before proceeding with the finding of these constants it is necessary to remember that the numerical values of ψ_x and ψ_y are not given at the same points in the field, for ψ_x is given along integer values of y but at half-integer points of x, while ψ_y is given along integer values of x but at half-integer values of y. The values of both "line" stream functions for each integer combination of the co-ordinates are therefore found by interpolation.

MEXICO

At every integer combination of the co-ordinates x and y there are now two numbers, representing the numerical values of the two line stream functions at these points. The symbols ψ_x and ψ_y represent these numerical values. To obtain from these two sets of numbers one set of numbers, having the numerical values of the complete stream function for the field, a constant a_i is added to each row of ψ_x's and a constant b_j is added to each column of ψ_y's, such that

$$\psi_{x_{i,j}} + a_i = \psi_{y_{i,j}} + b_j \quad . \tag{4}$$

The value of a_i may differ from row to row and b_j may differ from column to column.

The condition represented by equation (4) can only be satisfied if the field is an ideal nondivergent field. In actual practice random errors in observation, even of a nominal nondivergent field, make it impossible to satisfy the equation (4) exactly. Instead, it is necessary to find statistically the set of constants which most nearly satisfies equation (4). This may be done by imposing the condition that the square of the difference

$$(\psi_{x_{i,j}} + a_i) - (\psi_{y_{i,j}} + b_j)$$

be minimized, both along rows and along columns. This condition yields the four equations:

$$(5)\ (a)\quad \begin{aligned} &(i) && \frac{\partial}{\partial a_i} \sum_{j=1}^{n} \left\{ (\psi_{x_{i,j}} + a_i) - (\psi_{y_{i,j}} + b_j) \right\}^2 = 0 \\ &(ii) && \frac{\partial}{\partial b_j} \sum_{j=1}^{n} \left\{ (\psi_{x_{i,j}} + a_i) - (\psi_{y_{i,j}} + b_j) \right\}^2 = 0 \end{aligned}$$

$$(b)\quad \begin{aligned} &(i) && \frac{\partial}{\partial a_i} \sum_{i=1}^{m} \left\{ (\psi_{x_{i,j}} + a_i) - (\psi_{y_{i,j}} + b_j) \right\}^2 = 0 \\ &(ii) && \frac{\partial}{\partial b_j} \sum_{i=1}^{m} \left\{ (\psi_{x_{i,j}} + a_i) - (\psi_{y_{i,j}} + b_j) \right\}^2 = 0 \end{aligned}$$

which reduce to

$$(6)\quad \begin{aligned} &(a) && \sum_{j=1}^{n} \psi_{x_{i,j}} + na_i = \sum_{j=1}^{n} \psi_{y_{i,j}} + \sum_{j=1}^{n} b_j \\ &(b) && \sum_{i=1}^{m} \psi_{y_{i,j}} + mb_j = \sum_{i=1}^{m} \psi_{x_{i,j}} + \sum_{i=1}^{m} a_i \, . \end{aligned}$$

Since the stream function is contained as a differential in the field it may be changed by a constant amount without affecting the differential properties which define the field. Therefore, one of the constants, either for a row or a column, may be given an arbitrary value. Here let $a_1 = 0$; *i.e.*, for $x = 1$, $a = 0$. Then from (6a), at $i = 1$,

$$\sum_{j=1}^{n} b_j = \sum_{j=1}^{n} \psi_{x_{1,j}} - \sum_{j=1}^{n} \psi_{y_{1,j}} \tag{7}$$

and (6a) becomes

$$a_i = \frac{1}{n}\left\{\sum_{j=1}^{n} \psi_{y_{i,j}} - \sum_{j=1}^{n} \psi_{x_{i,j}} + \sum_{j=1}^{n} \psi_{x_{1,j}} - \sum_{j=1}^{n} \psi_{y_{1,j}}\right\}. \tag{8}$$

Once all of the a_i's are found from (8), values of b_j may be computed for each column from

$$b_j = \frac{1}{m}\left\{\sum_{i=1}^{m} \psi_{x_{i,j}} - \sum_{i=1}^{m} \psi_{y_{i,j}} + \sum_{i=1}^{m} a_i\right\}, \tag{9}$$

which follows from (6b).

If the horizontal velocity field under consideration were ideally nondivergent and free from observational error, then only one set of constants would have to be found, since either of the two relations,

$$(10) \qquad \text{or} \qquad \begin{aligned} &\text{(a)}\ \ \Psi\,(x,\,y)_{i,j} = \psi_{x_{i,j}} + a_i \\ &\text{(b)}\ \ \Psi\,(x,\,y)'_{i,j} = \psi_{y_{i,j}} + b_j \end{aligned}$$

should define the same scalar field and represent the actual values of the stream function. In practice, however, it will be found that these two functions are not exactly the same, and the amount by which they differ is indicative of how much the actual field departs from the assumed nondivergent field. If the function as defined by (10a) is partially differentiated in both the x- and y-directions, it would yield both the observed values of the velocity component $v(x, y)$, and the best fit to the observed field of the component $u(x, y)$ that would result in a nondivergent field. Likewise, if the function as defined by (10b) is partially differentiated with respect to x and y, then the observed values of the component $u(x, y)$ will be obtained, as well as a set of values for the component $v(x, y)$, which is the best fit to the observed set that would result in a nondivergent field. It is convenient to average these two values for Ψ and thus obtain one set of numbers at each point in the grid representing the numerical value of the "stream function" for the field. The stream function defined in this manner is only one type of "best fit" to the observed velocity field.

If, for some reason, it is felt that one component of the velocity is likely to be more representative than the other, then a weighted average of the two functions defined by equation (10) might be formed.

STREAMLINES FOR A GENERAL TWO-DIMENSIONAL DIVERGENT VELOCITY FIELD

It is theoretically possible to express the streamlines of any two-dimensional velocity field by a mathematical equation of the form

$$\Psi(x, y) = \text{constant}, \tag{11}$$

the various lines being distinguished by different values of the constant. The existence of this stream integral, Ψ, makes it theoretically possible to reduce the streamline problem to one of contouring a scalar field.

This cannot be accomplished, however, by direct measurements. The stream integral must be calculated from the velocity components. In order to do this, an integrating factor $\lambda(x, y)$ must be found for the equations

$$\frac{\partial \Psi}{\partial x} = -\lambda v, \qquad \frac{\partial \Psi}{\partial y} = \lambda u. \tag{12}$$

Such an integrating factor always exists, and can be found by solving the differential equation

$$\frac{\partial}{\partial x}(\lambda u) + \frac{\partial}{\partial y}(\lambda v) = 0. \tag{13}$$

Since u and v are given only at discrete grid points, (13) must be solved numerically for λ. The values for λ are then inserted in (12), and these equations may be solved numerically for Ψ, the stream integral.

Inseparable from the solution for λ and Ψ is the problem of smoothing the data. The formal solution to this general problem has been indicated by Dr. Carl Eckart (personal communication). However, it does not appear likely that the equations can be solved in practice without the aid of modern electronic computing machines, and this is economically feasible only for large amounts of data.

APPLICATION TO SHIP'S SURFACE CURRENT OBSERVATIONS

Certain semiobjective aids in the construction of streamlines have been suggested (for example, see Bjerknes, 1911). In seeking a procedure whereby subprofessional personnel could prepare reproducible streamline charts, however, these methods do not suffice. The general solution to the stream integral problem seems at present too difficult to place on an economical computation basis. The method developed for a nondivergent velocity field may be applied, however, to those parts of the ocean where the divergence term is small and of a random nature.

It is the author's opinion that over certain large areas of the ocean the vertical shear of the vertical velocity component is a small and random term compared to the effects of the horizontal velocity field. Hence, in constructing streamlines for average velocity data, such as the monthly average surface currents for one-degree quadrangles prepared by the Hydrographic Office, the horizontal field may be assumed to be on the average a nondivergent field. This assumption would obviously fail in regions of known, large scale convergences or divergences.

Equations (3), (8), (9), and (10) have been employed in constructing the streamlines for two areas, one a 20 by 30 degree area in the Northwest Pacific, the other a 20 by 40 degree area including the Caribbean, the Gulf of Mexico, and part of the Saragasso Sea. This second case is given here as an example.

Hydrographic Current Chart Misc. No. 10,690-8 was used to obtain the basic data. It contains a velocity vector for every degree square. The grid of our model is in this case defined by the ½ degree lines of latitude and longitude. The Δy and Δx in equation (3) are each equal to one (degree). Fig. 1 is a chart of the area, and the vectors shown are the average of ships's surface current observations for the month of August.

The method of obtaining values of the stream function for contouring, as presented above, was tried for the entire area at once, with fair success in the Caribbean and the Florida Straits. The spread of the two functions defined by (10) was, however, quite large in the Gulf of Mexico, in the area off the west coast of Mexico, and in the Saragasso Sea region. The region was then broken up into five overlapping subregions, each subregion encompassing as little land as possible. The Gulf of Mexico was not included in this determination. Equations (3), (8), (9) and (10) were employed for each of the subregions. The areas were then fitted together, making use of the overlapping portions. The spread between the two functions defined by (10) was in almost all cases very small, and the subregions fitted together with but little break in continuity. The numbers in the center of each degree square in Fig. 1 represent the average of the two values of the stream function as given by (10a) and (10b). The streamlines, representing the contours of the average value of the stream function, are also shown in Fig. 1.

This application of the method of constructing streamlines indicates that it is best to subdivide fairly large areas into overlapping regions about 10 or 15 degrees square. Little additional labor is involved in breaking up the area, and the checking of the computations is made easier. The method appears to present a procedure whereby subprofessional personnel may prepare reproducible streamline charts of large ocean areas with but little professional supervision.

ACKNOWLEDGMENTS

Thanks are extended to Mrs. Alfreda Nixon and Miss Viola Bush for their assistance in carrying out the computations involved in testing the method. Dr. H. U. Sverdrup and Dr. Walter Munk gave considerable encouragement towards seeking a solution to this problem. I especially appreciate the time given by Dr. Carl Eckart in clarifying the over-all problem and in pointing out the relation of this special solution to the general case.

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Contribution No. 385

A MODEL OF THE VERTICAL STRUCTURE OF MASS IN EQUATORIAL WIND-DRIVEN CURRENTS OF A BAROCLINIC OCEAN[1]

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A model for the vertical distribution of density, which approximates observed conditions in the equatorial Pacific Ocean, is presented. This consists of a homogeneous layer near the surface overlying a baroclinic medium wherein the density varies exponentially in such a manner as to approach a constant value with increasing depth. It is shown that the depth of the upper homogeneous layer can be considered as a function only of the wind stress which is exerted upon the sea surface. The relationship is developed from Sverdrup's (1947) theory of wind-driven currents in a baroclinic ocean, where it has been demonstrated that the mean *horizontal* distribution of mass of the upper 1,000 meters is determined by the wind stress. The mean horizontal distribution of mass is, in turn, directly related to the depth of the homogeneous layer. Consequently, it is possible to describe the *three-dimensional* distribution of density and pressure, provided that the wind stress is known.

The distribution of density in a vertical section is constructed for the case of an east-west wind stress whose magnitude varies sinusoidally with latitude. The computed model is compared with a similar cross section of density obtained from oceanographic observations in the eastern Pacific.

THEORY

Review. In a baroclinic ocean the horizontal pressure gradient and velocity generally vanish at great depth. If d (a constant) is the selected depth of no motion and $p = p(xyz)$ is the pressure, then the

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vertical integral of pressure $P = P(xy)$, which represents the mean horizontal distribution of mass, is defined by

$$\frac{\partial P}{\partial x} \equiv \int_{\text{Surface}}^{d} \frac{\partial p}{\partial x} \cdot dz \,, \quad \frac{\partial P}{\partial y} \equiv \int_{\text{Surface}}^{d} \frac{\partial p}{\partial y} \cdot dz \,, \tag{1}$$

where z is the vertical co-ordinate measured downward from a reference near the surface. For unaccelerated motion in a baroclinic ocean, free of lateral friction and transient changes of density, it can be shown on the basis of Sverdrup's (1947) theory that the quantity $P(xy)$ is given by the expression

$$P = (x - x_o)\left[\bar{\tau}_x - \frac{\partial \bar{\tau}_x}{\partial y} R \cdot \tan \phi\right] + \int_{y_1}^{y} \tau_y\,(y')\,dy' \,, \tag{2}$$

where $\bar{\tau}_x = \bar{\tau}_x(xy)$ and $\tau_y = \tau_y(y)$ are the x and y components of wind stress, respectively, in a rectilinear system where x and y are the horizontal co-ordinates positive to the east and north, respectively, with the origin on the equator. The term ϕ is the latitude, positive north of the equator, and R is the mean radius of the earth. The zero subscript refers to the continental boundary, and the *bar* superscript indicates an average value over the range x to x_o. The limit y_1 represents an arbitrary limit. Expression (2) is valid provided (a) that a constant depth of no motion, d, does exist, (b) that a north-south vertical boundary is present, and (c) that τ_y is independent of x.

It can be shown that (2) is a very good approximation for the eastern equatorial Pacific, even where x_o—the co-ordinate of the American continental boundary—varies with latitude.

The Model. The selected density structure is essentially a generalization of the simple two layer system treated by Defant (1936), where the upper homogeneous layer is retained. The structure is as follows: there is [1] an upper homogeneous layer of depth $h = h(xy)$ and density ρ_o; beneath this is [2] a baroclinic transitional layer extending from h to depth d, below which the water is at rest and of constant density ρ_d. An exponential transition will be assumed, such that the density $\rho(xyz)$ approaches ρ_d asymptotically with increasing depth, in good approximation of the model. One possible form is

$$\rho\,(xyz) \equiv \rho_2 = \rho_d - \Delta\rho e^{1-z/h} \,, \; z \geqslant h \,, \tag{3}$$

where $\Delta\rho = \rho_d - \rho_o$. The model is illustrated in Fig. 1, in which it is compared with actual distributions of ρ with depth, for various values of h. From (3) it is possible to solve for the P-function in terms of h.

To a very close degree of approximation the pressure is given by the hydrostatic equation,

$$p = g \int_{-\zeta}^{z} \rho\,(xyz)\,dz\,, \tag{4}$$

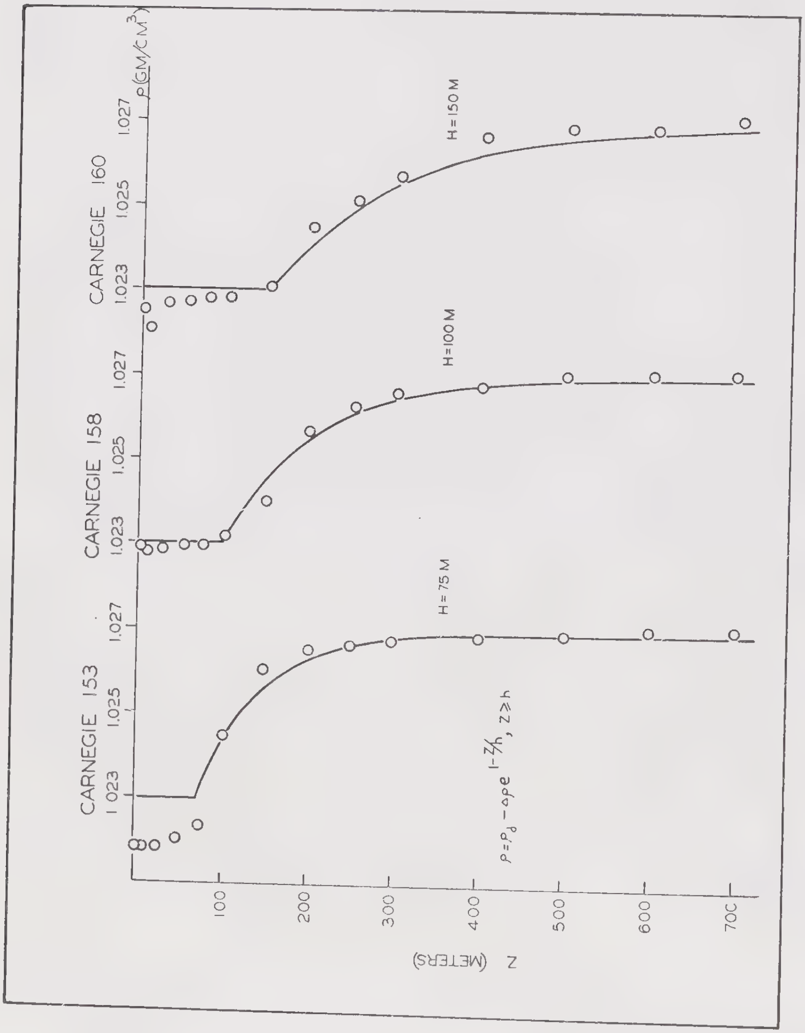

Figure 1. Comparison of observed densities (neglecting compressional effect) for three Carnegie stations in the Pacific with the computed vertical distribution of density for various values of *h*.

where $\zeta = \zeta(xy)$ is the *elevation* of the surface, and g is the acceleration of gravity.

It will be convenient to deal with the space derivatives of pressure rather than with the pressure itself. The pressure gradient in the x-direction is given by

$$\left(\frac{\partial p}{\partial x}\right)_1 = g\frac{\partial}{\partial x}\int_{-\zeta}^{z}\rho_o dz = g\rho_o\frac{\partial\zeta}{\partial x}, \quad -\zeta \leqslant z \leqslant h, \tag{5}$$

in the upper layer, and by

$$\left(\frac{\partial p}{\partial x}\right)_2 = g\left[\rho_o\left(\frac{\partial\zeta}{\partial x} + \frac{\partial h}{\partial x}\right) - \rho_d\frac{\partial h}{\partial x} + \Delta\rho\frac{\partial}{\partial x}\left(he^{1-z/h} - h\right)\right], \quad z \geqslant h, \tag{6}$$

in the transition layer. Similar expressions are valid for $\partial p/\partial y$.

At $z \geqslant d$, the pressure gradient vanishes, and if $d >> h$, (6) yields the approximation

$$\zeta = \frac{2\Delta\rho}{\rho_o}h, \tag{7}$$

provided that the reference level is selected properly. Both h and ζ must either be positive or vanish.

The derivative of integrated pressure is, from (1), (6) and (7)

$$\frac{\partial P}{\partial x} = \int_{-\zeta}^{h} g\rho_o\frac{\partial\zeta}{\partial x}\cdot dz + \int_{h}^{d} g\Delta\rho\frac{\partial}{\partial x}\left(he^{1-z/h}\right)\cdot dz\,.$$

This yields the approximation

$$\frac{\partial P}{\partial x} = \frac{5g\Delta\rho}{2}\frac{\partial h^2}{\partial x}\,.$$

A similar expression holds for $\partial P/\partial y$, and it follows

$$P = \frac{5}{2}g\Delta\rho\cdot h^2 + \text{constant}. \tag{8}$$

The Sinusoidal Wind Stress Distribution. The east-west component of wind stress in the equatorial Pacific has been shown to vary nearly sinusoidally with latitude (Reid, 1948). It will be assumed here for simplicity that

$$\bar{\tau}_x = \tau_x = \tau_o + b\sin\omega\left(\phi - \phi_o\right), \tau_y = 0, \tag{9}$$

where τ_o, b, ω, ϕ_o are constants. The function P and consequently h

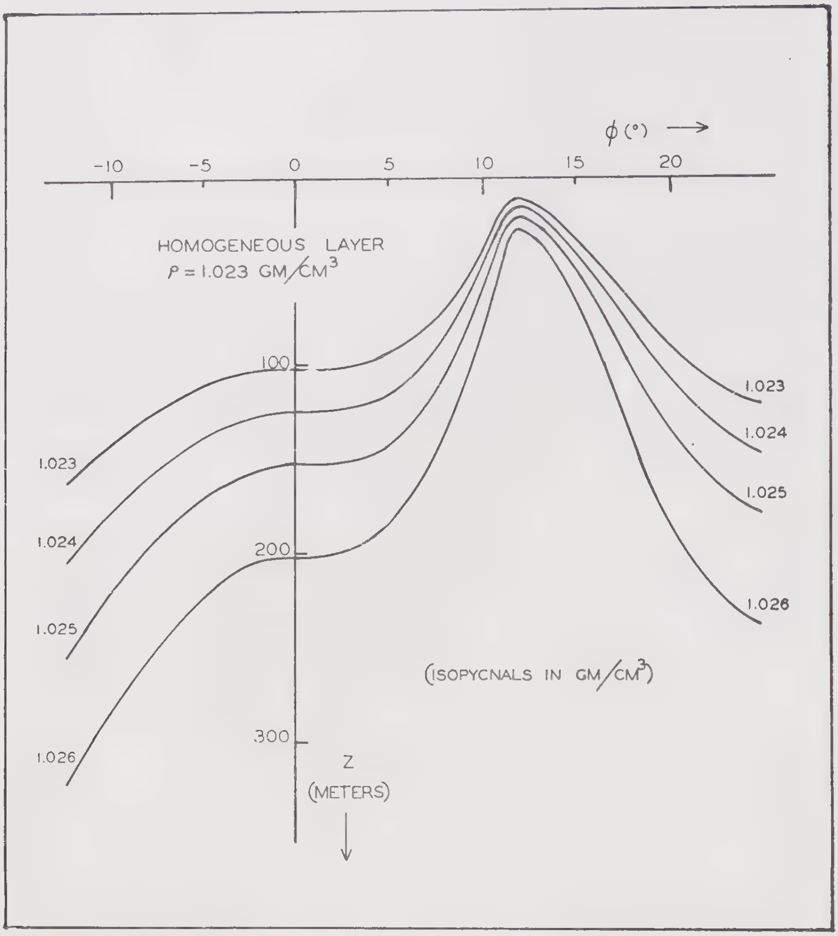

Figure 2. The computed distribution of density along the Carnegie section of the central equatorial Pacific, derived from the hypothetical exponential density model and the sinusoidal wind stress distribution.

can be evaluated in terms of the position co-ordinates. Using (2), (8), and (9) it follows

$$h^2 = \frac{2}{5g\Delta\rho}(x - x_o)\left[\tau_o + b\sin\omega(\phi - \phi_o) - \omega b\tan\phi\cdot\cos\omega(\phi - \phi_o)\right] - K, \qquad (10)$$

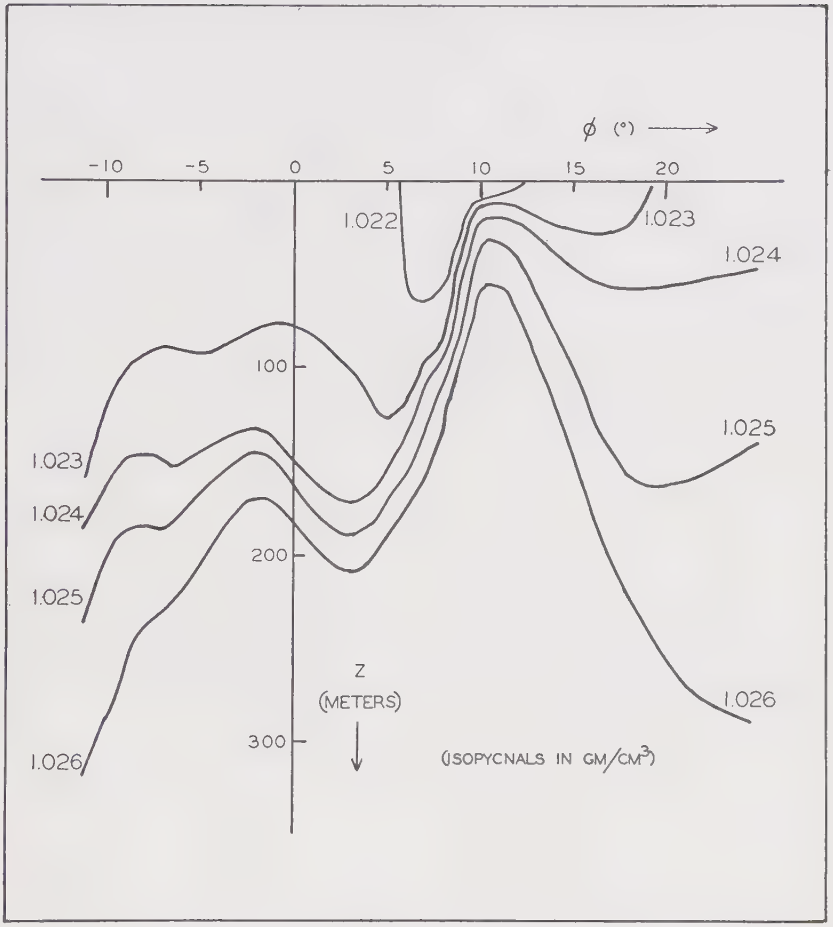

Figure 3. The actual distribution of density along the CARNEGIE section of the central equatorial Pacific, derived from oceanographic data.

and the surface elevation is

$$\zeta^2 = \frac{8\Delta\rho}{5g\rho_o^2}(x - x_o)\left[\tau_o + b\sin\omega(\phi - \phi_o) - \omega b\tan\phi\cdot\cos\omega(\phi - \phi_o)\right] - \left(\frac{2\Delta\rho}{\rho_o}\right)^2 K, \qquad (11)$$

where K is the constant of integration, to be selected such that h is always a real quantity.

It is evident that h^2 and ζ^2 *increase linearly* with distance from the boundary for the chosen distribution of density and wind stress.

The Pressure Distribution. The form of the pressure distribution is obtained readily from the hydrostatic equation and the model (3), giving

$$\left.\begin{aligned} & p_1 = g\,(\rho_o z + 2\Delta\rho h),\; -\zeta \leqslant z \leqslant h, \\ \text{and} \quad & p_2 = g\,(p_d z + \Delta\rho h e^{1-z/h}),\; z \geqslant h. \end{aligned}\right\} \tag{12}$$

The slope of the isosteres, $i\rho_2$, in the transition layer can be shown to be

$$i\rho_2 = \left(\frac{z}{h}\right) i_h\,, \quad z \geqslant h\,, \tag{13}$$

where i_h is the slope of the interface at $z = h$. It can be verified that the isobaric slopes, i_p, for the two layers are

$$\left.\begin{aligned} & i_{p_1} = -\frac{2\Delta\rho}{\rho_o}\, i_h = i_\zeta\,, \\ \text{and} \quad & i_{p_2} = -\frac{\Delta\rho}{\rho}\left(1 + \frac{z}{h}\right)e^{1-z/h}\, i_h \doteq \frac{1}{2}\left(1 + \frac{z}{h}\right)e^{1-z/h}\, i_{p_1}\,. \end{aligned}\right\} \tag{14}$$

The isobaric slope in the transition layer is opposite in sign to the slope of h for all $z \geqslant h$. The isosteric slope, on the other hand, has the same sign as that of h for $x \geqslant h$. This clearly demonstrates the baroclinicity of the model fluid, *i. e.*, the isosteres intersect the isobars at all $z \geqslant h$.

It is evident from (14) that the isobaric slope becomes vanishingly small as z approaches d, which is necessary to satisfy the condition of stationary water below d.

DISCUSSION

The observations utilized in the computations consist essentially of a line of 13 stations between Lat. 24° 57′ N, Long. 137° 44′ W and Lat. 10° 54′ S, Long. 161° 53′ W, occupied by the CARNEGIE between October 21 and November 4, 1929 (Fleming, *et al.*, 1945).

A value of K was selected as 3.8 x 10^8 so that the minimum value of h for the model would correspond to that observed at about Lat. 13° N. The depth of no motion was taken as 700 m, and the mean values of ρ_o and ρ_d were taken for the Pacific data as 1.0230 and 1.0274 gm/cm^3, respectively.[2]

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[2] The values represented here do not include the effect of compression, nor does the model. The effect is unimportant, since there is very little contribution to the gradients of p and P due to compression.

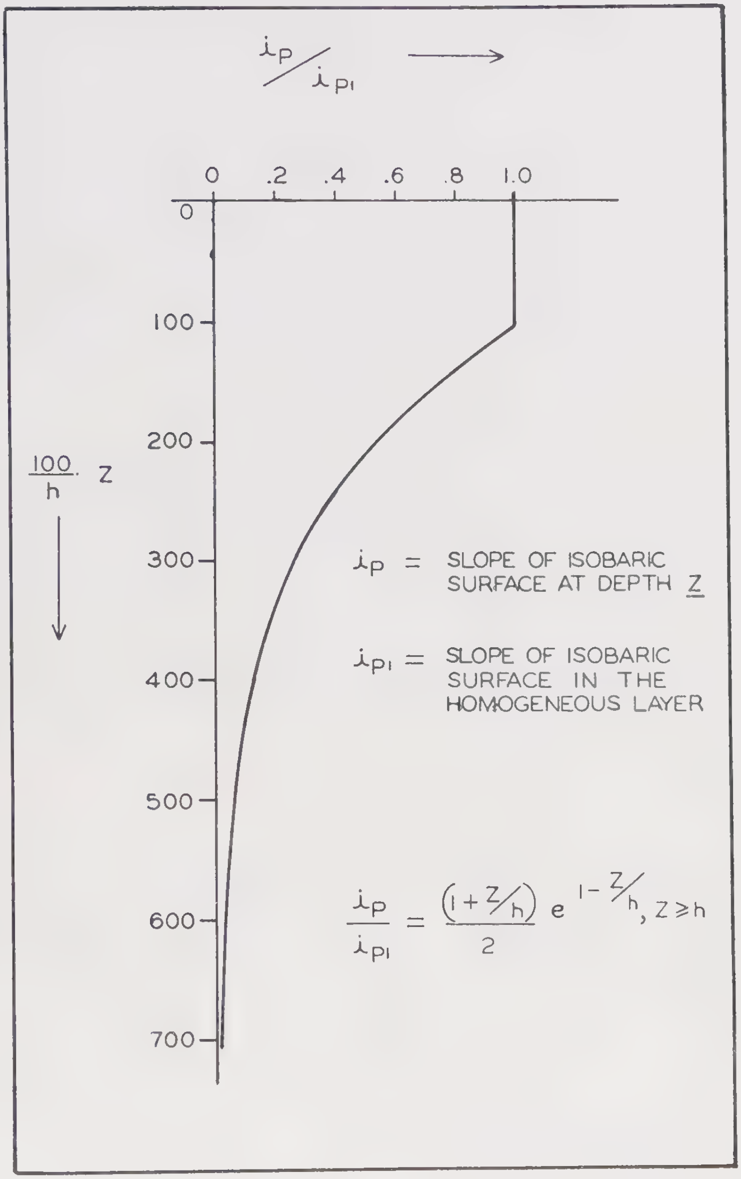

Figure 4. The dependence of isobaric slope on depth, for the exponential density distribution. The ratio of the slope to that in the homogeneous layer is plotted vs. depth in per cent of the homogeneous layer depth.

The values of the wind stress constants are:

$$\tau_o = -0.3\ \text{dyne/cm}^2,\ \omega = 13.85,$$
$${}_b = \ \ 0.3\ \text{dyne/cm}^2,\ \phi_o = 1^\circ.$$

The hypothetical vertical density structure along the CARNEGIE section computed from expressions (3) and (10) and the above constants is shown in Fig. 2. The values of $(x - x_o)$ were obtained from the position of the CARNEGIE stations and the American continental boundary. The actual distribution of density, omitting effects of compression, is shown in Fig. 3 for comparison. A plot of the vertical variation of isobaric slope, obtained from (14), is shown in Fig. 4. There is no discontinuity in the slope at $z = h$, as in the case of the simple two layer system [where $\rho(z)$ is discontinuous].

SUMMARY AND CONCLUSIONS

The exponential transition of density below a light homogeneous layer is strikingly representative of the vertical distribution of density in the equatorial Pacific. From this model and the theory of wind-driven currents, the entire field of density and pressure is described. A cross section of the model density structure is compared with the actual distribution given by the CARNEGIE data. The principal characteristics of the observed structure of mass are accounted for in the model, except in the vicinity of the equator.

The conditions at the equator need further consideration, especially regarding the role of thermodynamic processes in determining the distribution of the P-function.

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Contribution No. 386

DIATOM POPULATIONS ASSOCIATED WITH EDDIES OFF SOUTHERN CALIFORNIA IN 1941[1]

By

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INTRODUCTION

During 1941 the E. W. SCRIPPS made ten cruises off southern California, each covering the same area of about 80,000 square kilometers. The cruise plan consisted of a grid of approximately 40 stations. At each station a catch was made with the Allen five-liter closing bottle every ten meters from the surface to 60 meters. The catch was filtered through a net of No. 25 silk bolting cloth, and the diatoms so collected were later identified, counted and recorded as the number of diatoms per liter. The laboratory work was done by the late W. E. Allen, who had no opportunity to prepare more than a general report, which is now being edited for publication. For the purpose of this paper the number of diatoms per liter is taken as representing the number per square centimeter from the level at which the catch was made to the level of the next catch ten meters below. The sum of the seven catches at a station represents, according to this convention, the diatom population per square centimeter to a depth of 70 meters. Collections were not made at greater depths. However, the progressive reduction of the population down to 60 meters suggests that the diatoms below this depth would not change the totals sufficiently to affect the validity of the arguments presented here.

At each station, observations were made of temperature, salinity, and oxygen to a depth of 500 meters. Dynamic height anomalies (Sverdrup, 1947) are shown on all charts of this report as an indication of the character of the surface water and its horizontal movements. The general dynamic features of these waters have been discussed by Sverdrup and Fleming (1941), who showed that in the spring and early summer two types of surface water (down to about 100 meters) are present in this area: (1) "new" water which has been recently drawn to the surface by upwelling and (2) "old" water which has been

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at the surface for a relatively long time. New water is characterized by low temperature, high salinity, and a shallow thermocline. At this time of year there is typically in the western part of the cruise area and beyond it a south-flowing current of old water. Along its left-hand boundary one or more cyclonic eddies of new water appear, and inshore from these there may be a current of old water flowing northwesterly. Sverdrup and Fleming discussed the evidence for the theory that the two oppositely-directed currents represent two sides of a single large eddy. The pattern of circulation outlined above becomes less evident as upwelling of new water diminishes later in the year.

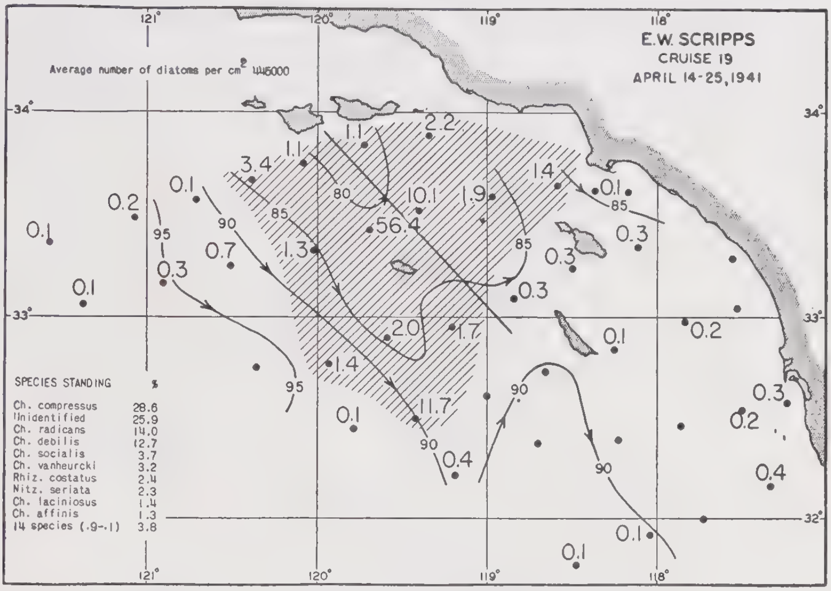
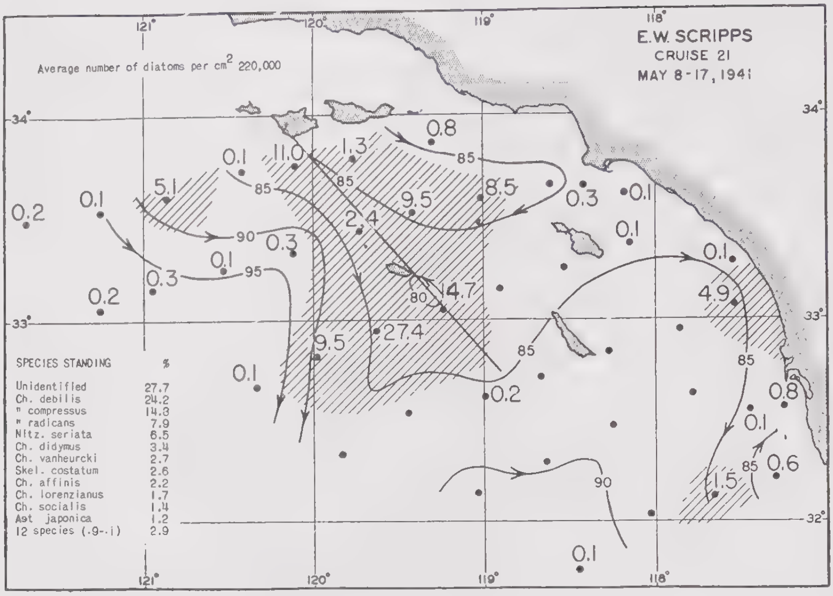

E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
Average number of diatoms per cm² 446000
121°
120°
119°
118°
34°
33°
32°
SPECIES STANDING %
Ch. compressus 28.6
Unidentified 25.9
Ch. radicans 14.0
Ch. debilis 12.7
Ch. socialis 3.7
Ch. vanheurcki 3.2
Rhiz. costatus 2.4
Nitz. seriata 2.3
Ch. laciniosus 1.4
Ch. affinis 1.3
14 species (.9-.1) 3.8
0.1
0.2
0.1
0.1
95
0.3
90
0.7
3.4
1.1
1.1
2.2
80
85
10.1
1.9
56.4
1.3
1.4
0.1
85
0.3
85
0.3
0.3
2.0
1.7
0.1
0.2
1.4
95
0.1
11.7
90
0.4
90
90
0.3
0.2
0.4
0.1
0.1

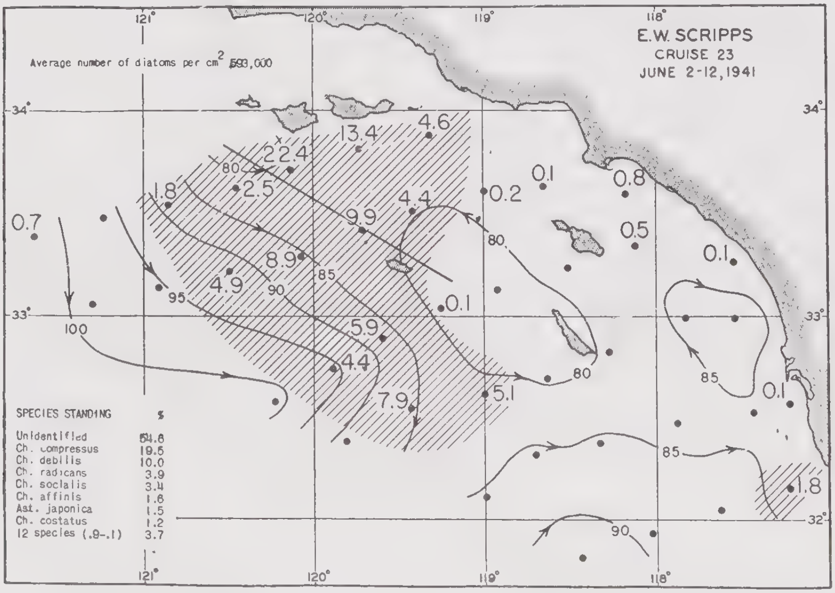
Figure 1. Distribution of diatoms and hydrography, Cruise 19. At each station (indicated by a dot), phytoplankton catches were made every ten meters from the surface to 60 meters. Figures at stations show percentage contribution of each station to cruise total of diatoms. Hatched area includes all stations contributing at least one per cent to cruise total. Numbered and arrowed contours show topography of sea surface in dynamic centimeters relative to 500 decibar surface. Arrows indicate inferred direction of flow of surface currents. Close spacing of contours indicates high current velocities (maximum velocities 8 miles per day).

Michael (1921) showed, for a line of stations extending 125 miles out from Point Fermin, a negative correlation between the population density of the phytoplankton and the temperature of the surrounding water, indicating that large populations are, on the average, found in


E.W. SCRIPPS
CRUISE 21
MAY 8-17, 1941
Average number of diatoms per cm^2 220,000
121°
120°
119°
118°
34°
33°
32°
0.8
0.1
11.0
1.3
85
5.1
9.5
8.5
0.3
0.1
0.2
0.1
90
2.4
0.3
0.1
0.1
95
0.3
14.7
80
0.2
0.1
4.9
9.5
27.4
85
85
0.1
0.2
0.8
0.1
85
0.6
1.5
90
0.1

SPECIES STANDING	%
Unidentified	27.7
Ch. debilis	24.2
" compressus	14.3
" radicans	7.9
Nitz. seriata	6.5
Ch. didymus	3.4
Ch. vanheurcki	2.7
Skel. costatum	2.6
Ch. affinis	2.2
Ch. lorenzianus	1.7
Ch. socialis	1.4
Ast japonica	1.2
12 species (.9-.1)	2.9

Figure 2. Distribution of diatoms, Cruise 21. See Fig. 1 for description.


E.W. SCRIPPS
CRUISE 23
JUNE 2-12, 1941
Average number of diatoms per cm^2 593,000
121°
120°
119°
118°
34°
33°
32°
13.4
4.6
22.4
80
2.5
0.1
0.8
0.2
1.8
4.4
0.7
9.9
0.5
80
8.9
0.1
85
4.9
90
95
0.1
100
5.9
4.4
80
85
5.1
0.1
7.9
85
1.8
90

SPECIES STANDING	%
Unidentified	54.8
Ch. compressus	19.5
Ch. debilis	10.0
Ch. radicans	3.9
Ch. socialis	3.4
Ch. affinis	1.6
Ast. japonica	1.5
Ch. costatus	1.2
12 species (.9-.1)	3.7

Figure 3. Distribution of diatoms, Cruise 23. See Fig. 1 for description.

recently upwelled water. Sverdrup and Allen (1939) found that large diatom populations in southern California waters were limited to new water, whereas water which had spent a long time on the surface was always characterized by a small diatom population.

OBSERVATIONS

For four cruises in 1941 Figs. 1 to 4 show the percentage contribution of each station to the cruise total of all diatoms. It is clear that the distribution of the diatom population is orderly and that the spacing of the stations is close enough to indicate the population at all points. In each figure, the area embracing all stations contributing at least 1% to the cruise total has been hatched. For convenience, the outline of this area will be called the one-per-cent contour.[2]

TABLE I. Distribution of Diatoms off Southern California in 1941

Cruise	*Month*	*Av. No. of diatoms per station (thousands per cm²)*	*No. of stations occupied*	*No. of stations with 1% or more of total population*	*% of total population at these stations*
17	March	1020	41	21	95.9
19	April	445	41	13	95.7
21	May	220	42	11	95.8
23	June	593	40	13	97.9
25	June	493	40	10	96.4
27	July	51	41	21	96.2
28	August	500	38	15	94.0
30	September	378	33	21	96.0
32	October	131	38	23	97.9
33	November	8	33	15	94.3

As shown on Table I, this contour encloses more than 90% of all the diatoms observed on each cruise. Fig. 5 shows that the use of either the half-per-cent or the two-per-cent contour would not greatly change the proportion of the population enclosed. For instance, the half-per-cent contour would enclose an additional 39 stations (four

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[2] This outline can be defined precisely (on the assumption that the number of diatoms changes gradually from station to station) as the locus of all points such that if a station had been occupied at any one of them it would have contributed one per cent to the cruise total. The cruise total is the sum of the station populations. The station population has already been defined as the population to 70 meters per cm² of surface. The cruise total multiplied by the average area represented by one station (about 2,000 km²) equals the total population in the whole area covered by the cruise.

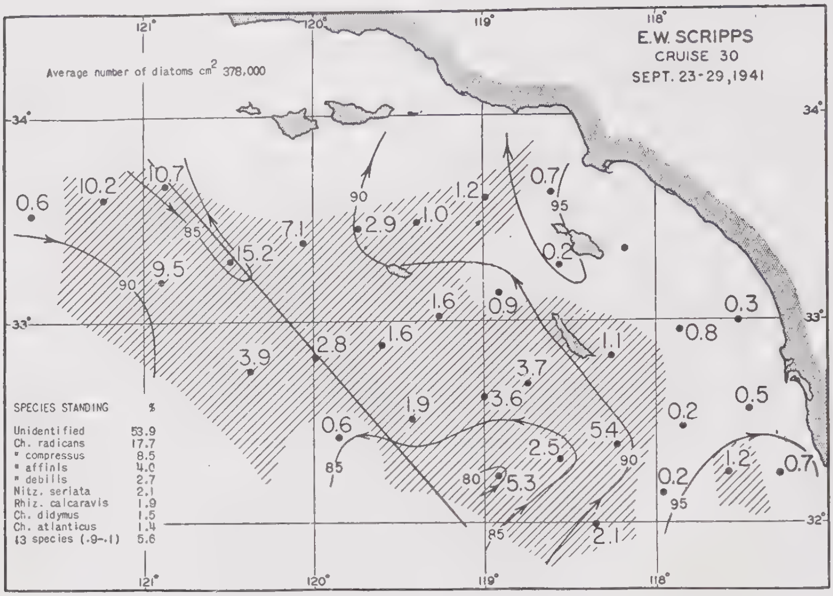
E.W. SCRIPPS
CRUISE 30
SEPT. 23-29, 1941
Average number of diatoms cm² 378,000
121°
120°
119°
118°
34°
33°
32°
0.6
10.2
10.7
85
15.2
7.1
9.5
90
3.9
2.8
1.6
2.9
1.0
1.2
0.7
95
0.2
1.6
0.9
1.1
3.7
3.6
1.9
0.6
85
2.5
5.4
90
80
5.3
85
2.1
0.3
0.8
0.2
0.5
0.2
95
1.2
0.7
SPECIES STANDING %
Unidentified 53.9
Ch. radicans 17.7
" compressus 8.5
" affinis 4.0
" debilis 2.7
Nitz. seriata 2.1
Rhiz. calcaravis 1.9
Ch. didymus 1.5
Ch. atlanticus 1.4
13 species (.9-.1) 5.6

Figure 4. Distribution of diatoms, Cruise 30. See Fig. 1 for description.

stations per cruise) and would increase the enclosed population by about 5% per cruise. On the other hand, use of the two-per-cent contour would exclude 49 stations (five per cruise) included by the one-per-cent contour and would diminish the enclosed population by about 6% per cruise. Neither alternate line would affect the conclusion that nearly all of the diatom population during these cruises was found regularly in a single sharply defined area of limited extent.

During most of the 1941 cruises, particularly in the spring and early summer months, a moderately intense cyclonic eddy was prèsent in the northern part of the cruise area. In Figs. 1 to 4, lines have been drawn through the centers of such eddies, in a direction parallel to the flow of the offshore current, or if this could not be determined, in a southeasterly direction. In most cruises these lines divided the populations in such a way that the larger part was on the offshore (southwest side) of the line. Except during cruises 27, 32, and possibly 30, over half of all the diatoms collected occurred in these very restricted patches (Table IIA). In the exceptional cruises the eddies were close to the outermost line of stations, so that it is likely that the area of densest population was not sampled at all. Thus, it appears that the cyclonic eddies in the northern parts of the area characteristically condatine large diatom populations which were especially dense in the

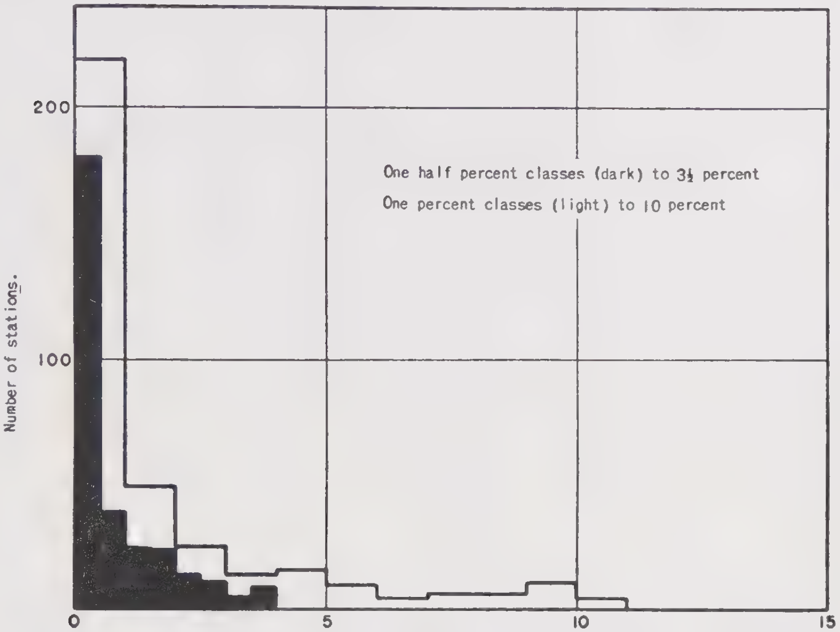

Figure 5. Frequency distribution of contributions of individual stations to cruise totals of all diatoms. The shaded histogram shows stations contributing less than 4%. The open histogram shows stations contributing less than 11%. Ten stations, each contributing more than 11%, are not included.

offshore half of the eddies (Table IIB). As this water flowed southeastward the populations developed and then were scattered or destroyed. Whether the greatest development was reached before or after the water entered the cruise area from the northwest is unknown, but the rapid decay and almost total disappearance of the population within the local waters is shown by the paucity of diatoms just outside of the eastern, southern and western boundary to the productive area.

This pattern of population densities remained approximately constant throughout the year, although the total population varied from cruise to cruise (Table I) and although the species of diatoms involved varied in relative abundance from season to season. During several cruises a single species accounted for more than a quarter of the entire population, and in every cruise a dozen species or less comprised from one-third to nine-tenths of the population. Seasonal succession and other changes in the composition of the list of leading species shown on the charts (Figs. 1 to 4) are matters to be discussed at length elsewhere.

TABLE II. Distribution of Diatoms in Cyclonic Eddies off Southern California

	A		B	
Cruise	*No. of stations inside 1% contour and in south-western half of cyclonic eddy*	*% of total population at these stations*	*Av. % of total population at each station inside 1% contour*	*Av. % of total population at each station inside 1% contour and in south-western half of eddy*
17	10	64.1	4.6	6.4
19	8	79.0	7.4	9.9
21	4–5	50.3–65.0	8.7	12.5
23	9–10	51.3–73.7	7.5	5.7
25	7	80.5	9.6	11.5
27	8	16.4	4.6	2.1
28	7–8	51.3–60.8	6.3	7.3
30	3–6	23.6–52.3	4.6	7.9
32	8	37.3	4.2	4.7
33	11	81.1	6.3	7.4

The point to be made here is that, although the composition of the population changed, the pattern as a whole bore a remarkable constant relationship to the hydrography.

In the present report we will describe in detail only the observations made during the spring months when conditions were most clearcut and uniform from cruise to cruise. Therefore, discussion will be limited to those observations, and especially to those of cruise 19, which was representative of the spring cruises.

A number of the individual species observed during cruise 19 were distributed in patterns as clearly related to the hydrography as that of the diatom population as a whole. Figs. 6 to 11 show the distribution of six separate species during this cruise. As in previous charts, the hatching covers those stations contributing at least one per cent to the cruise total for the species. It is clear that *Nitzschia seriata* (Fig. 6) and *Chaetoceros radicans* (Fig. 7) had essentially the same distribution as the whole diatom population, as did *C. lorenzianus, N. longissima,* and several minor species. The boundaries of the area of high population were not determined, then, by a single preponderant species. As suggested by Michael, a whole group of species appears to be controlled in the same way by the same set of factors.

A second type of distribution is that of *C. socialis* (Figs. 10, 14). This species and *C. compressus* (Fig. 11), *C. debilis* (Fig. 15) and *C. didymus* were very similar in being restricted essentially to a few sta-

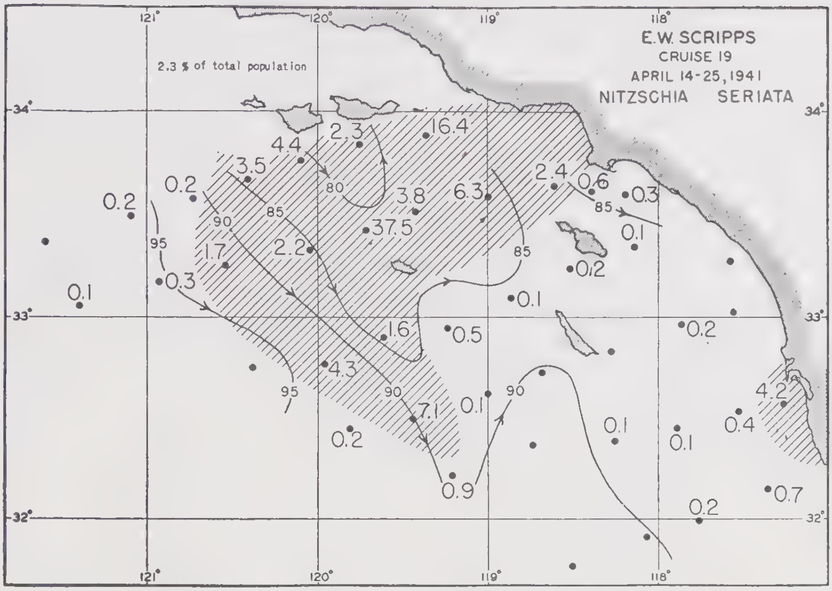
E.W. SCRIPPS
CRUISE 19
APRIL 14-25,1941
NITZSCHIA SERIATA
2.3 % of total population
121°
120°
119°
118°
34°
33°
32°
0.2
0.1
0.2
0.3
3.5
4.4
2.3
16.4
1.7
2.2
37.5
3.8
6.3
2.4
0.6
0.3
0.1
0.2
0.1
1.6
0.5
4.3
7.1
0.1
0.2
0.9
0.1
0.1
0.4
4.2
0.2
0.7
0.2
95
90
85
80

Figure 6. Distribution of *Nitzschia seriata*, Cruise 19. At each station (indicated by a dot), phytoplankton catches were made every ten meters from the surface to 60 meters. Figures at stations show percentage contribution of each station to cruise total of the species. Hatched area includes all stations contributing at least one per cent to cruise total.

tions within the one-per-cent contour. Of these four species, all but *C. didymus* represented important fractions of the total diatom population, as shown in Fig. 1. At station 24 (Lat. 33° 25′ N, Long. 119° 43′ W) more than two-thirds of the cruise total for each of these species was collected, and they were also abundant at station 46 (Lat. 32° 29′ N, Long. 119° 26′ W). These species were common only in the neighborhood of these two stations, and in general they were not observed at all outside of the one-per-cent contour for all diatoms.

A radically different kind of distribution is that of *Rhizosolenia alata* (Fig. 8). The distribution of this species, as well as *Dactyliosolen antarcticus* (Fig. 9), *Rhizosolenia hebetata, Chaetoceros dadayi, C. atlanticus* and *C. messanensis*, is complementary to that of the main group. On the whole, diatoms of these six species were few or absent at populous stations but were relatively numerous at many stations outside the populous areas.

Thus, many of the species collected during cruise 19 can be divided into groups according to their distribution as follows:

1. Common, occurring at most stations in the eddy but rarely elsewhere. *Chaetoceros radicans*, etc.

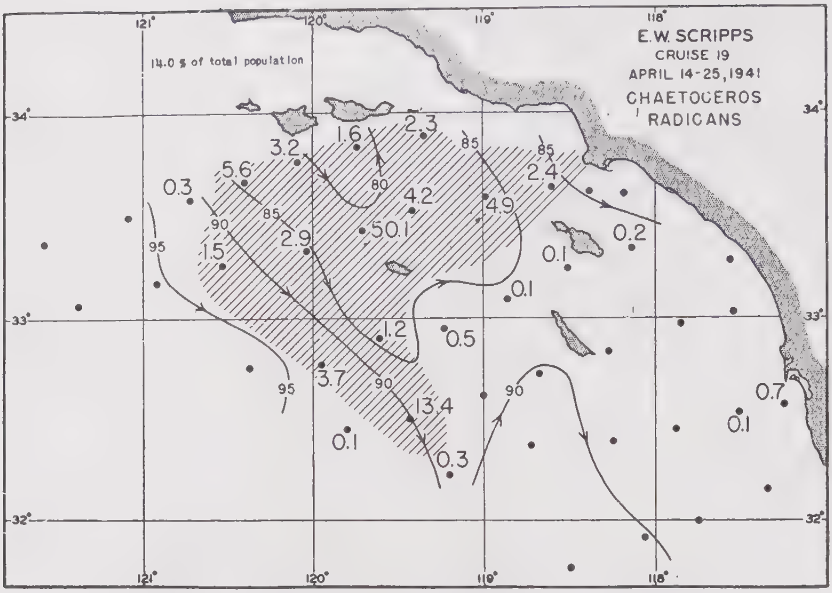
E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
CHAETOCEROS RADICANS
14.0 % of total population
121°
120°
119°
118°
34°
33°
32°
1.6
2.3
3.2
85
85
5.6
2.4
0.3
80
4.2
90
85
4.9
50.1
95
2.9
0.2
1.5
0.1
0.1
1.2
0.5
3.7
90
95
90
0.7
13.4
0.1
0.1
0.3

Figure 7. Distribution of *Chaetoceros radicans*, Cruise 19.

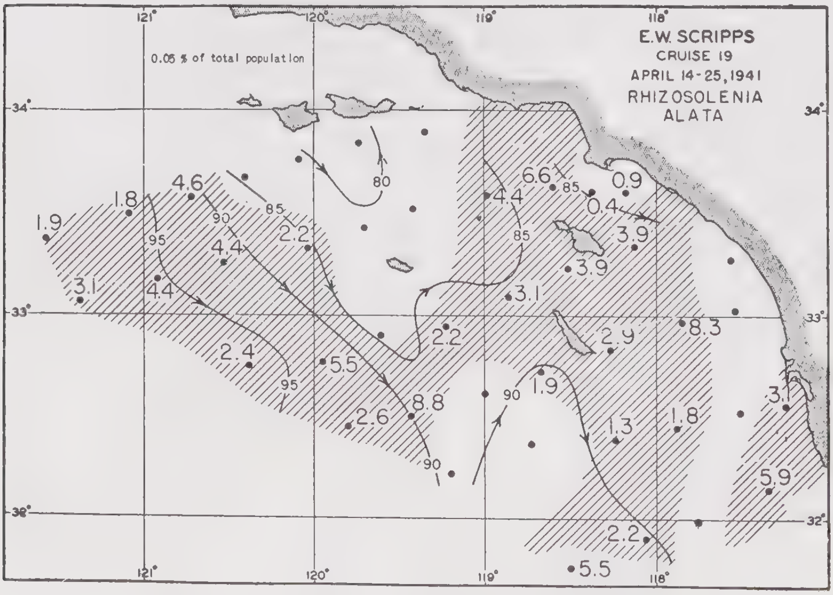
E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
RHIZOSOLENIA ALATA
0.05 % of total population
121°
120°
119°
118°
34°
33°
32°
80
6.6
85
0.9
4.6
4.4
1.8
85
0.4
1.9
90
95
2.2
85
3.9
4.4
3.9
3.1
4.4
3.1
8.3
2.2
2.9
2.4
5.5
95
90
1.9
3.1
8.8
2.6
1.3
1.8
90
5.9
2.2
5.5

Figure 8. Distribution of *Rhizosolenia alata*, Cruise 19.

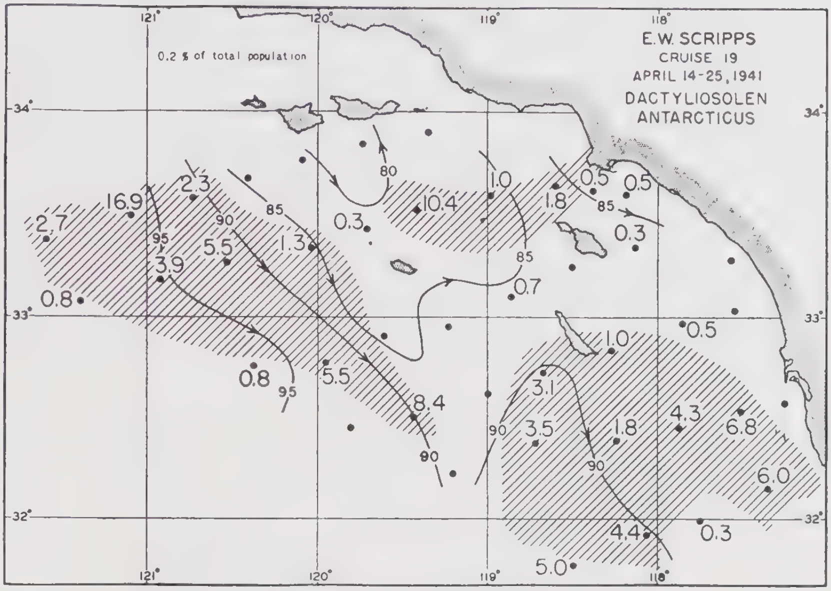
E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
DACTYLIOSOLEN
ANTARCTICUS
0.2 % of total population
121°
120°
119°
118°
34°
33°
32°
2.7
16.9
2.3
0.8
3.9
5.5
1.3
0.3
10.4
1.0
1.8
0.5
0.5
0.3
0.7
0.8
5.5
8.4
1.0
0.5
3.1
3.5
1.8
4.3
6.8
6.0
4.4
0.3
5.0
80
85
90
95

Figure 9. Distribution of *Dactyliosolen antarcticus*, Cruise 19.

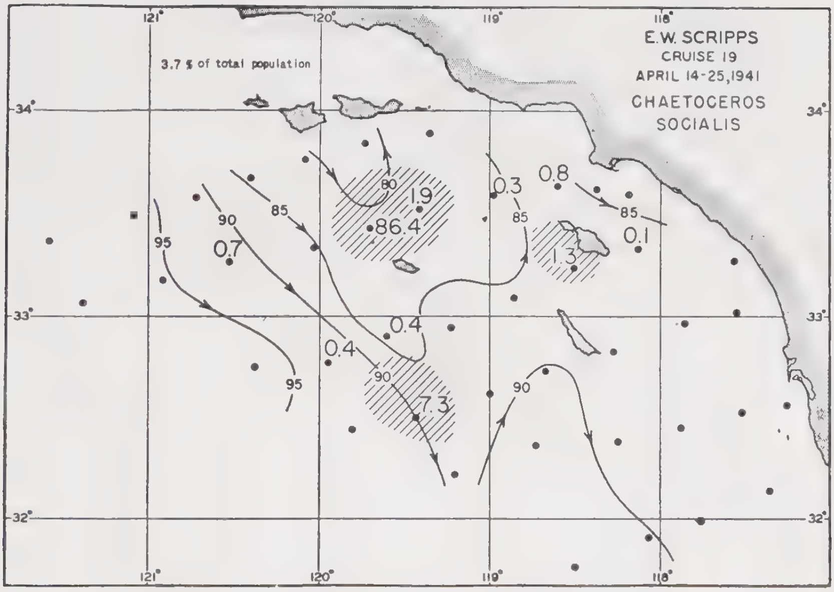
E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
CHAETOCEROS
SOCIALIS
3.7 % of total population
121°
120°
119°
118°
34°
33°
32°
0.7
1.9
86.4
0.3
0.8
0.1
1.3
0.4
0.4
7.3
80
85
90
95

Figure 10. Distribution of *Chaetoceros socialis*, Cruise 19.

2. Restricted, occurring at only a few stations in the cyclonic eddy. *Chaetoceros socialis*, etc.
3. Complementary, occurring seldom within the eddy, but generally elsewhere. *Rhizosolenia alata*, etc.

Species intermediate in character between those of groups 1 and 2 are to be expected, and it is not unlikely that an extensive study would show that the distribution of some species changes with, for instance, the seasons. However, all species listed above retained their characteristic distribution throughout the spring cruises of 1941. Many other species observed are not readily fitted into this scheme. In particular, some were so scarce that it is only possible to conclude that they did poorly over the entire cruise area.

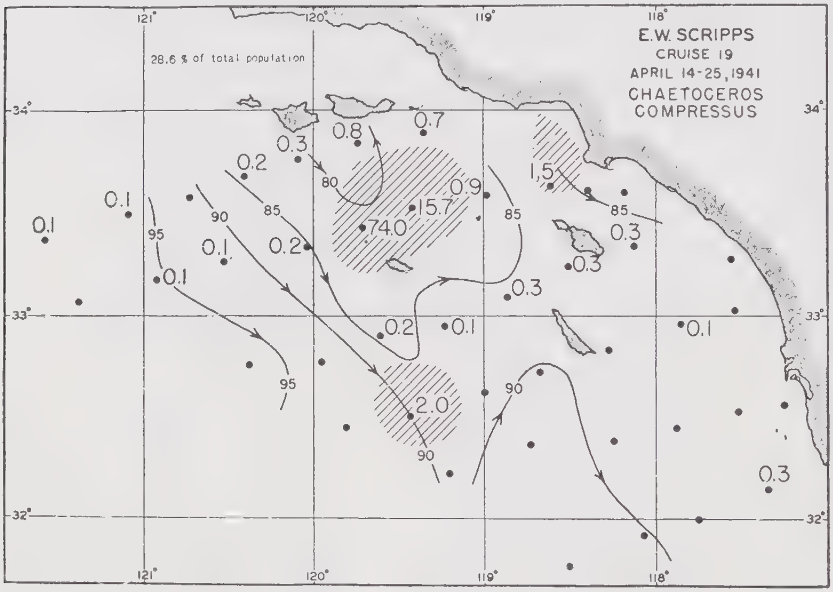
E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
CHAETOCEROS
COMPRESSUS
28.6 % of total population
121°
120°
119°
118°
34°
33°
32°
0.1
0.1
0.1
0.1
0.2
0.3
0.8
0.7
0.9
15.7
74.0
0.2
0.2
0.1
1.5
0.3
0.3
0.3
0.1
2.0
0.3
95
90
85
80
85
85
95
90
90

Figure 11. Distribution of *Chaetoceros compressus*, Cruise 19.

If data for other years substantiate this division, each of the groups can be considered as belonging to a "plankton element" defined by Gran (1902: 74 ff) as an assemblage having similar ecological requirements. Since Gran's paper, many such ecological requirements have been discovered and elucidated, particularly by Harvey (1947, and papers referred to therein).

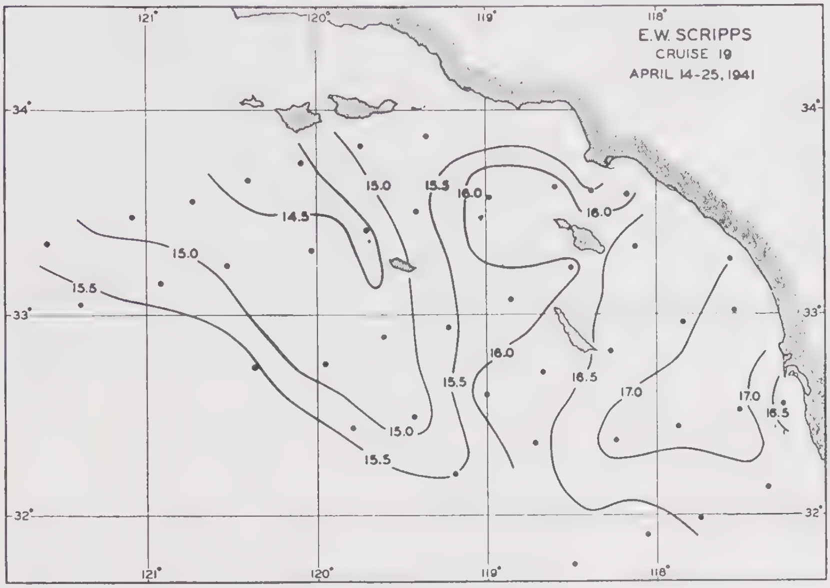
121°
120°
119°
118°
E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
34°
33°
32°
15.0
15.5
16.0
14.5
16.0
15.0
15.5
16.0
15.5
16.5
17.0
17.0
16.5
15.0
15.5
121°
120°
119°
118°

Figure 12. Surface temperatures, Cruise 19.

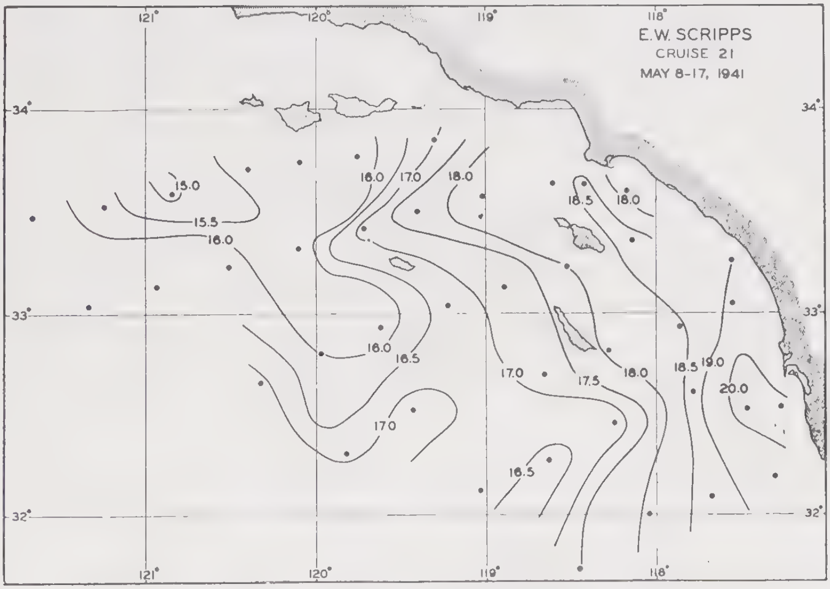
121°
120°
119°
118°
E.W. SCRIPPS
CRUISE 21
MAY 8-17, 1941
34°
33°
32°
15.0
15.5
16.0
16.0
17.0
18.0
18.5
18.0
16.0
16.5
17.0
17.5
18.0
18.5
19.0
20.0
17.0
16.5
121°
120°
119°
118°

Figure 13. Surface temperatures, Cruise 21.

INTERPRETATION

A close relationship existed between these groups of plankton and the circulation features of the water. It is inconceivable that the small differences in temperature observed, or possible small differences in average insolation, could account for the distribution of the diatoms. The depth of the mixed layer, which increased with distance from shore, as Sverdrup and Fleming observed, could not by itself account for the distribution. Rather, it is necessary to look for a complex of physical, chemical and biotic factors whose individual values and combined effect varied from day to day and from point to point. The over-all effect is that freshly upwelled water is more fertile than old water, as pointed out by Michael (1921) and by Moberg (1928). The details of the distribution of the diatoms during the spring of 1941 can be related to this phenomenon as follows.

Freshly upwelled water entered the area of observations from the northwest intermittently, and its concentration in some areas was higher than elsewhere as indicated by low temperatures in the centers of the cylonic eddies (Figs. 12, 13). In these areas, as at stations 24 and 46 in cruise 19, large populations occurred, with species in groups one and two predominating. From the fact that the very densely populated stations, which were also the only stations at which group-two diatoms were found in appreciable numbers, often occurred singly or in pairs, it can be inferred that the diameter of the areas of highest concentration of upwelled water were close to the station grid interval of 20–30 kilometers. Surrounding these areas was a larger one in which the concentration of new water diminished with increasing distance from the centers of population, as indicated by higher temperatures and lower salinities. This area supported a large population in which the species of group one were conspicuous, while diatoms of group two were rare or absent. The remainder of the area covered by the cruises was, on the whole, occupied by water which was of high temperature and low salinity and therefore had probably been on the surface for some time. The diatom population was small, but species of group three were found in their greatest abundance here.

The diminution in population density was probably controlled by different combinations of factors in different parts of the eddy system. Toward the east, that portion of the upwelled water which was carried around the eddy, except near its periphery, had little opportunity for mixing with old water, and the diminution of the population in the inshore half of the eddy must have resulted from processes occurring within the water body, such as exhaustion of nutrients, increase of grazing, etc., which produced combined effects as shown by Braarud

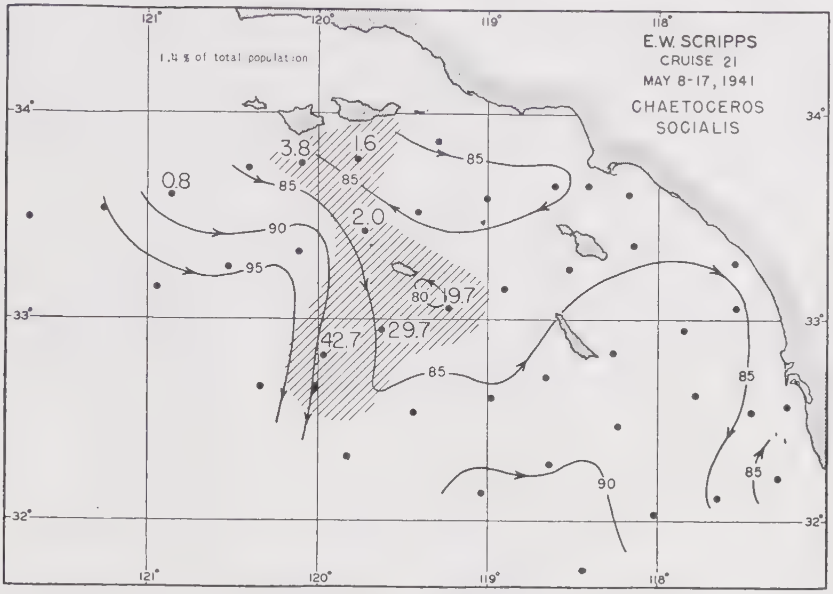
121°
120°
119°
118°
E.W. SCRIPPS
CRUISE 21
MAY 8-17, 1941
CHAETOCEROS
SOCIALIS
1.4 % of total population
34°
33°
32°
3.8
1.6
85
85
85
0.8
2.0
90
95
80
19.7
42.7
29.7
85
85
90
85

Figure 14. Distribution of *Chaetoceros socialis*, Cruise 21.

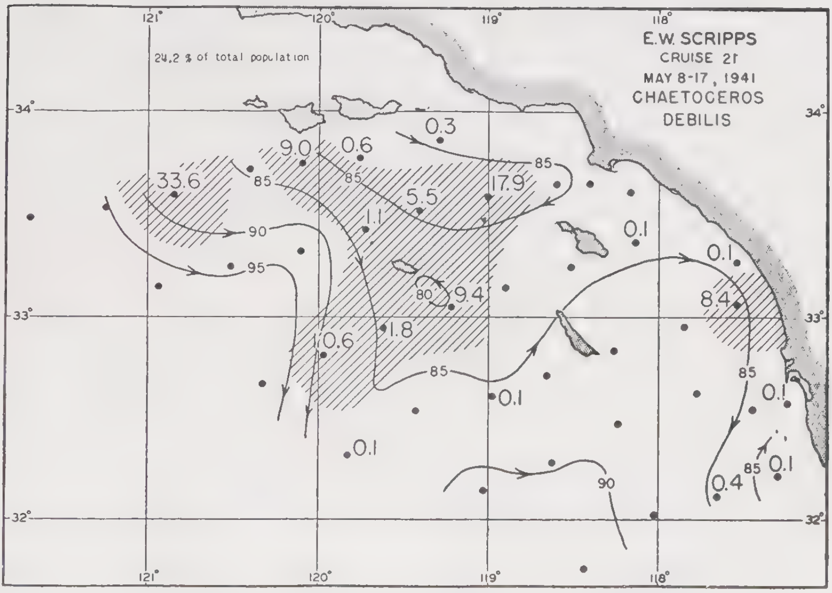
121°
120°
119°
118°
E.W. SCRIPPS
CRUISE 21
MAY 8-17, 1941
CHAETOCEROS
DEBILIS
24.2 % of total population
34°
33°
32°
0.3
9.0
0.6
85
33.6
85
85
5.5
17.9
1.1
90
0.1
95
0.1
80
9.4
8.4
10.6
1.8
85
85
0.1
0.1
0.1
85
0.1
0.4
90

Figure 15. Distribution of *Chaetoceros debilis* Cruise 21.

(1935) and Fleming (1939). To the west, intense lateral mixing with offshore water which was both infertile and barren (Sverdrup and Fleming, 1941: 331) would reduce both the concentration of nutrients and the density of the population, and, in combination with the other processes, produce the steep population gradient on the offshore side of the eddies.

SUMMARY

In waters off southern California in 1941, the diatom population was concentrated at any one time in one or a few relatively small patches. These patches were closely related to cyclonic eddies of freshly upwelled water entering the area of observation from the north (particularly in the spring when upwelling was strongest). The population was most abundant in the offshore halves of the eddies where the upwelled water, judged by its low temperature and estimated path of travel, was most concentrated and had been present on the surface the shortest time. Populations in water which had apparently travelled some distance around the eddies were less abundant, presumably because of exhaustion of nutrients, grazing, and other biological processes. Abundance diminished more sharply to the west than to the east because, in addition, there was intense lateral mixing with barren infertile offshore water.

Four plankton elements, in the sense of Gran, could tentatively be identified: (1) a group of species, mostly very abundant, found only where the upwelled water was most concentrated; (2) a group, some very abundant, found at almost all stations within the well marked patches of generally high population density; (3) a group of species, none of which reached great abundance but which were relatively more abundant in water which had been on the surface a long time; and (4) a group of species rare throughout the cruise area.

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Contribution No. 387

EVIDENCE OF WORLD-WIDE SUBMERGENCE[1]

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INTRODUCTION

At the beginning of the century geologists were discussing the idea that the glacial period was the result of enormous vertical movements of the continents. Uplifts were said to have cooled the climates, bringing on glaciation, and subsequent submergence caused the glaciers to melt. This hypothesis was supported by the finding of deep canyons on the sea floor which indicated the former elevated condition of the continents. The idea was later abandoned, partly because of the very limited amount of information concerning submarine canyons but largely because the glacial period was found to have a series of ice stages or epochs with intervening times of relatively warm climate. The alternate elevation and depression of the continents to a degree sufficient to produce widespread glaciation, all during about one million years, appeared to be completely out of accord with the history which geologists had been building from their accumulating evidence.

The abandonment of the diastrophic hypothesis seems to have resulted in shelving the subject of submarine canyons, so that for a quarter of a century there was almost no mention of them in the literature. This neglect terminated when the amazing advances of hydrographic surveys of the past two decades revealed the presence of abundant submarine canyons of huge dimensions off many coasts of the world. While many geologists have considered these canyons as having been cut by running water, and therefore being indicative of great changes of level, others have developed hypotheses by which they attempted to explain the canyons as having been formed under the ocean. These explanations have proved satisfactory to many geologists, but as oceanographic research has progressed it has become increasingly evident that the submarine canyons are remarkably like the river-cut canyons of the land. During the same time, an abundance of field observations has supplied independent evidence that

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there has been a very general submergence of continental borders, oceanic islands, and perhaps even of the deep sea bottom.

SUBMARINE CANYONS

Nature of Canyons. Because of the implications of enormous changes of level resulting from the world-wide distribution of the canyons, if they prove to be submerged stream valleys, some assurance should be provided that they are truly stream-eroded rather than the product of processes which can operate on the sea floor. If one considers the number of illustrious scientists who have offered hypotheses attempting to prove a submarine origin, skepticism of the stream origin would be natural. However, if one studies the detailed charts of the canyons and examines the evidence which has come from canyon exploration by dredging, coring, bottom photography, current measurements, and diving, the skepticism should not be as great. In fact, a study of the field data leaves one with the impression that the various authors of hypotheses of submarine origin were describing somewhat imaginary undersea valleys.

Submarine canyons have been described from many parts of the world (Fig. 1). Canyons have been discovered on virtually all well-explored continental slopes except where there are indications of relatively recent faulting or where the slopes are very gentle. Further exceptions may exist off coasts which now have very slight precipitation.

Some writers have been inclined to consider that the canyons were entirely different in character in different areas. For example, they have been quite willing to concede that the California canyons were the result of stream erosion, while they considered that the canyons in most other areas were of a different nature. In the present article the canyons can not be discussed adequately, so that reference should be made to a recent comparison of canyons from all parts of the world (Shepard, 1948: 210–229). So far as evidence is now available, the conclusion from this work is that the canyons are essentially the same the world over. They cut the submarine slopes as deep notches with *V*-shaped transverse profiles. They have narrow floors sloping almost continuously away from the lands. They have twisting courses and tributaries entering with the dendritic pattern characteristic of land canyons. The walls are precipitous and have proved to contain rock exposures in almost all of the areas from which samples are available. Many of the rocks are of a type resistant to erosion. The majority of the canyons extend shoreward across most of the continental shelf and many of them enter estuaries. Others, however, have their heads on

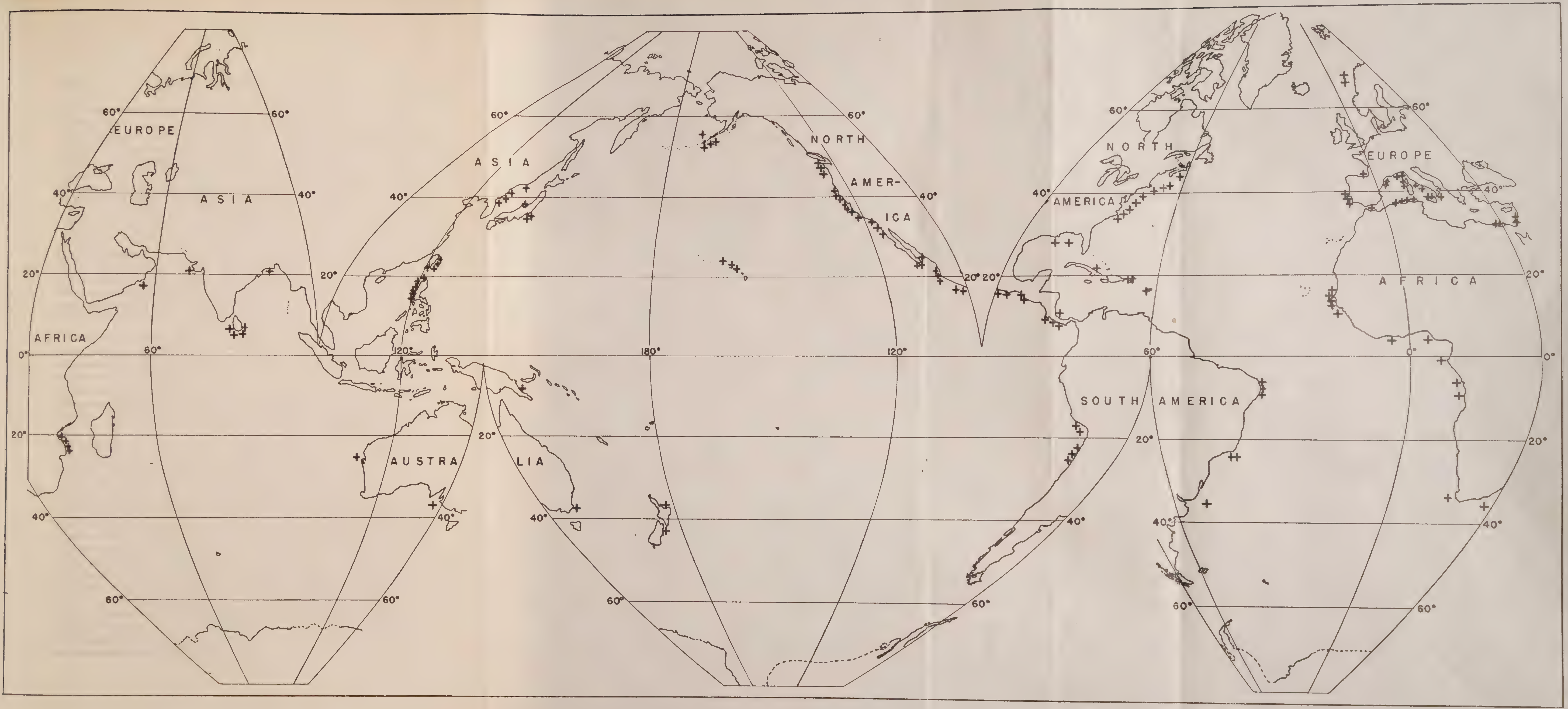
EUROPE
ASIA
AFRICA
ASIA
AUSTRALIA
NORTH AMERICA
NORTH AMERICA
SOUTH AMERICA
EUROPE
AFRICA
60°
40°
20°
0°
20°
40°
60°
60°
120°
180°
120°
60°
0°

Figure 1. The world distribution of submarine canyons. Each cross indicates one or a group of canyons. Many areas lack adquate soundings for the determination of canyons.

the outer shelves far from land or on the upper portions of the continental slopes.

The canyons can be traced outward to depths of many hundreds of fathoms. The outer terminations of most canyons can not be ascertained from available evidence. In some cases they show a change from a *V* shape to a trough shape at depths of the order of 1,000 fathoms. Off southern California some of them appear to end with flats or submerged deltas at depths which are approximately those of the rim of the basin into which the canyon has been cut.

The most completely studied canyons have proved to be identical in character to the land canyons which are directly inside (Fig. 2). Frank Haymaker of the Scripps Institution has dived into and explored the head of two canyons at La Jolla, California. He found typical stream erosion features, such as staircase canyons with waterfall drops, hanging valleys, tributaries entering at grade, vertical and even overhanging rock walls, and cobble covered floors. The canyons on land inside have all of these same features.

Possible Submarine Origins. So many types of submarine origin have been suggested for canyons that it is difficult to discuss each adequately in the present paper. A few of the principal hypotheses will be mentioned briefly.

The idea that the canyons are the result of faulting or rifting (Wegener, 1922: 177, 178) seems to have been developed without any apparent knowledge of their character. Fault valleys are obviously unlike the canyons just described. The former are in general straight-sided, flat-floored, free of tributaries, and have deep basin depressions. The faulting origin is not now seriously considered by any one acquainted with the subject of submarine canyons.

The idea of submarine artesian spring sapping (Johnson, 1939) seems also to be based on very little other than the conviction that other hypotheses are inadequate. The idea depends largely on the presence of good aquifers outcropping on the continental slopes, with the circulation of water undermining the slope and thus forming gullies which might be enlarged by landslides. However, the canyons are by no means confined to the slopes, since most of them, as explained previously, cross the shelves and many extend into estuaries. Furthermore, the rock on the walls of the canyons does not favor the aquifer idea. Nor do the canyon floors have the large sinks or basins which would be developed by underground water. The possibility for artesian circulation under many of the areas where canyons exist is negligible. For example, in some places faults intervene at the coast preventing any appreciable circulation of this sort.

The conception of origin by tsunamis (tidal waves) (Bucher, 1940) seems to be equally unfortunate. The great waves, set up rarely by submarine faulting, are virtually confined in their effects to the shore and coast. Although the tsunamis develop strong currents in shallow water along the shore, their effectiveness decreases rapidly with depth. In long waves of the Stokes type, the horizontal bottom velocity under the crests of the waves where it reaches a maximum of short duration, is given by the formaula: $Q = CH/(2h)$, where Q is the velocity of the bottom current, C is the wave velocity, H is the wave height and h is the depth of water. To obtain the wave velocity, use is made of the formula $C = \sqrt{gh}$, where g is the acceleration of gravity. Using these formulae and considering a very large tsunami, we find that the maximum currents would have values approximately as follows:

Fathoms	*Cm/sec*
5	95
10	62
100	11
300	4.5
500	3

These figures indicate how powerless tidal waves are in producing erosion in deep areas. Furthermore, several areas which have an abundance of tsunamis have no canyons, as for example the Sanriku Coast of Japan.

The only hypothesis which has been supported in print by more than one geologist is that of cutting by density currents (Daly, 1936). According to this idea heavy muddy water moves down slopes, thereby excavating the canyons. The hypothesis has some appealing features, since these density currents are actually known to exist, at least in lakes. Model studies show how the currents produced by heavily weighted liquids could cut gullies into soft materials. Beyond this point the hypothesis has been built on highly hypothetical claims. It has been said that density currents flow along the bottom of Lake Mead at the rate of four miles an hour. Actually, the basis for this rate has been shown by the U. S. Reclamation Service to be groundless, and the present studies of Lake Mead by the U. S. Geological Survey show that the density currents are so feeble that they are allowing the rapid deposition of clay at the front of the delta of the Colorado River where the currents are best developed. In fact, at the places where density currents should be at their best, deposition is going on rapidly. This being the case, one should hesitate to believe that canyons thousands of feet deep cut into hard rocks could be due to such currents.

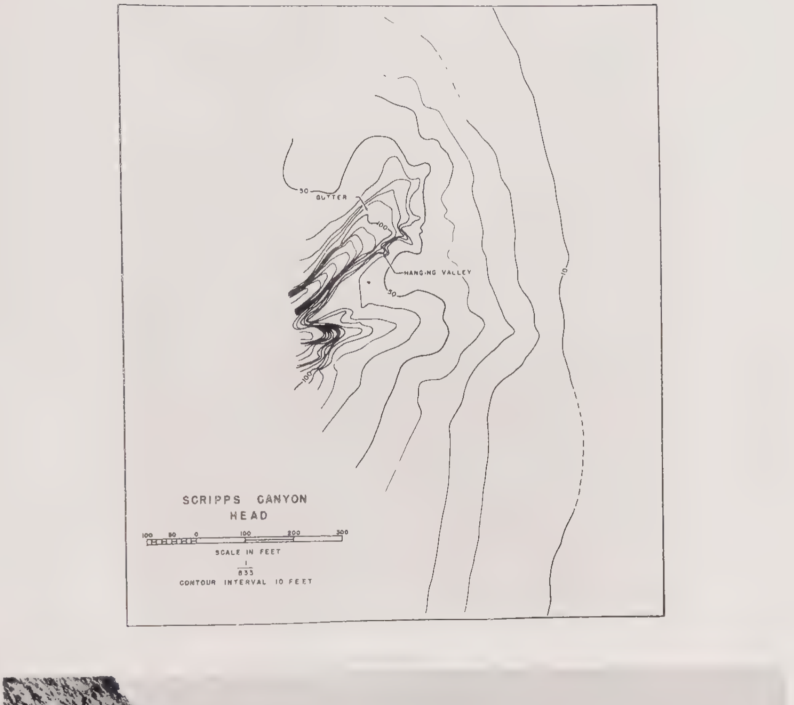
SCRIPPS CANYON HEAD
30
GUTTER
100
HANGING VALLEY
50
10
100
100 50 0 100 200 300
SCALE IN FEET
$\frac{1}{833}$
CONTOUR INTERVAL 10 FEET

Figure 2. Comparison between the submarine canyon head (upper) and an adjacent land canyon (lower) at La Jolla, California. Both canyons have hanging valleys and precipitous walls. The arrow in lower illustration indicates the edge of a 40 foot vertical cliff.

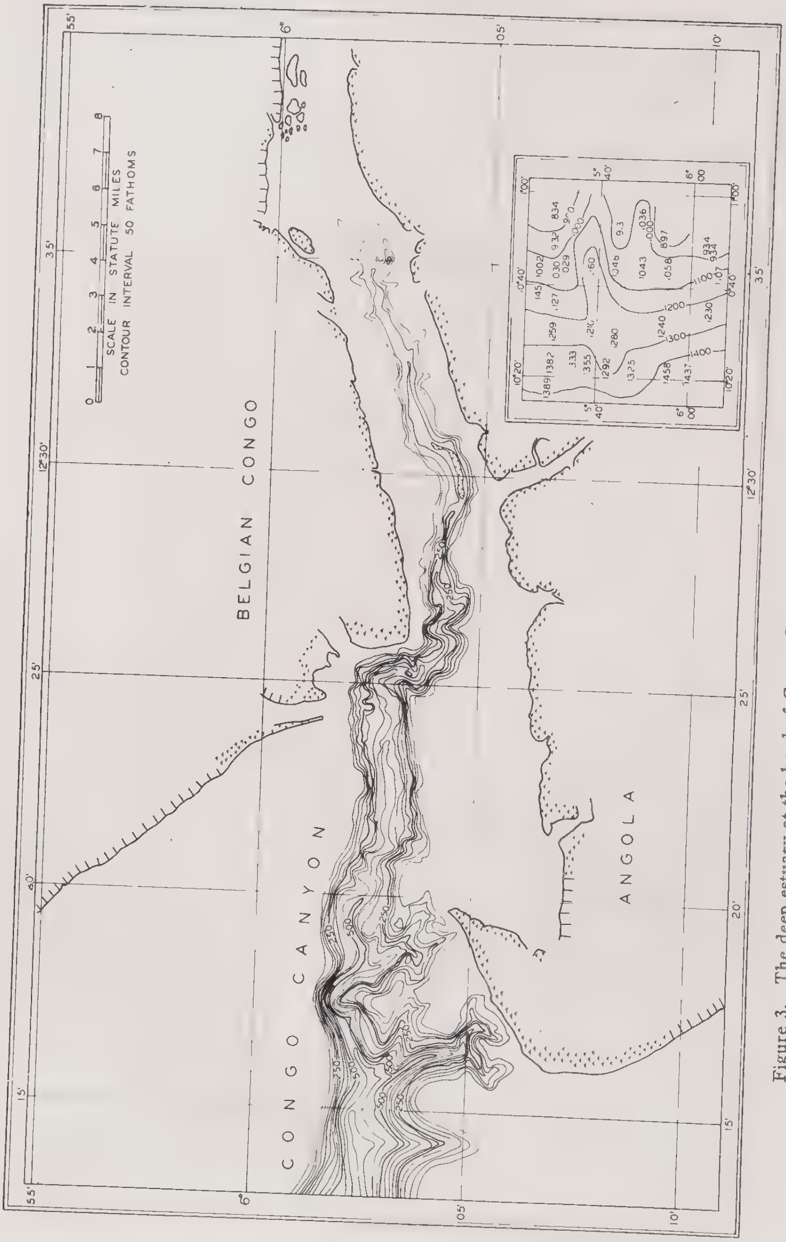
BELGIAN CONGO
ANGOLA
CONGO CANYON
SCALE IN STATUTE MILES
CONTOUR INTERVAL 50 FATHOMS
0 1 2 3 4 5 6 7 8
12°30'
35'
25'
20'
15'
55'
6°
05'
10'
250
500

Figure 3. The deep estuary at the head of Congo Canyon. The inset shows the outer canyon terminus.

Stream Origin and Landslide Clearing. Since none of the existing marine origin hypotheses can explain the characteristics of the canyons and since stream-cut canyons are essentially identical in character with the submarine types, the subaerial origin appears to be by far the most promising. It is possible, however, that currents now completely unknown have been the cause. Certainly, the currents now existing on the canyon floors are far too weak to be held responsible. These currents have been determined by current meter observations, and their nature is confirmed by diver reports. They are barely strong enough to keep the finer sediment in suspension except under unusual circumstances when they cease entirely.

Deposition is in progress in the canyons, as is now well known from the California studies. The canyon heads would soon be filled by this deposition if it were not for the instability of the fill. The mud in the sediments and the organic debris, particularly kelp and eel grass, apparently favor slumping along the inclines at the canyon heads so that the fill slides seaward periodically. Evidence both of the fill and of the slides comes from the repeated soundings along carefully surveyed lines. Slides have also been detected by sudden deepening at the ends of piers which had been built into the canyon heads. To date, there is no evidence that these slides do more than remove sediment from the canyon floors. It is possible that some enlargements may occur, particularly in the nature of widening, but it seems almost impossible that the huge canyons could have been cut thousands of feet into the solid rocks underlying the continental slopes by landsliding alone. The extension of a canyon 50 miles across the continental shelf and up into an estuary (Fig. 3) by landsliding is obviously out of the question. The shapes of the canyons are by no means those of landslide scars. The latter are for the most part cirque-like and have greater width than length. Also, landslide scars have irregular floors with many basins along their courses. The sliding associated with the canyons must be preservative and not formative.

Implications of the Stream Origin Hypothesis. Almost all objection to the subaerial origin of the canyons has come from concern over the implications which such an origin would have. If the canyons were found only off certain unstable coasts such as California or Japan, it might be easy to convince geologists that the canyons were submerged by regional earth movements, but the finding of these canyons off supposedly stable coasts as well as unstable coasts without indication of any preference for the one or the other has caused considerable uncertainty. It is not only necessary to account for the submergence of the continental margins by a mile or more, but also for the deep drowning of insular canyons. We find, for example, that the canyons are well developed in the mid-Pacific Hawaiian Islands (Fig. 4). Here they are found off the deeply eroded windward coasts of the older islands, but so far as is known they are not present off the coasts where there have been recent lava flows.

It might be argued that the canyons have been submerged from time to time in the remote geological past, but most of the evidence which we now possess favors relatively recent submergence. The existence of narrow gorges with vertical and overhanging walls is not indicative of very great age, since the burrowing and boring of organisms on the ocean bottom should be capable of reducing these slopes to moderate inclinations over the course of millions of years. Furthermore, some canyon walls are definitely known to contain Tertiary formations, ranging from Eocene to Pliocene. This suggests that at least the inner parts of many of the canyons were cut during the Pleistocene or Recent. The Tertiary formations incidentally are found off both the east and west coasts of the United States, so that the implications of recency are not confined to unstable coasts. A valley has been found to extend to a depth of 350 feet below sea level in the delta of the Mississippi. This valley was traced to a depth of 1,000 feet at the coast by an oil company using geophysical methods of exploration and later was traced across the shelf nearly to the point where the head of Mississippi submarine canyon appears on the charts. The age of the excavation of the filled head within the delta has been definitely determined by Fisk (1944: 11) to be late Pleistocene. By implication, the canyons which are cut into the edge of Georges Bank off the New England Coast are contemprary with the stand of the glaciers on these banks, since otherwise it would be difficult to imagine sufficient drainage from the small water sheds of the banks to cut canyons that are comparable in size with the canyons off the large river valleys from the Hudson to Chesapeake Bay. On the other hand, there is no evidence at present which would prove that more than the inner portions of the canyons down to depths of about 1,000 feet were cut during this late geological epoch. The deep outer portions may have been excavated at various times during the past and their filled heads reopened by excavation during the glacial period.

Conclusions Concerning Submarine Canyons. At the present stage of our canyon investigations we have found substantial evidence that the canyons are river-eroded whereas we have so far failed to find indications of submarine origin. The canyons are apparently present on both insular and continental slopes except where recent faulting or vulcanism has interfered, or where the slopes are so gentle that valleys

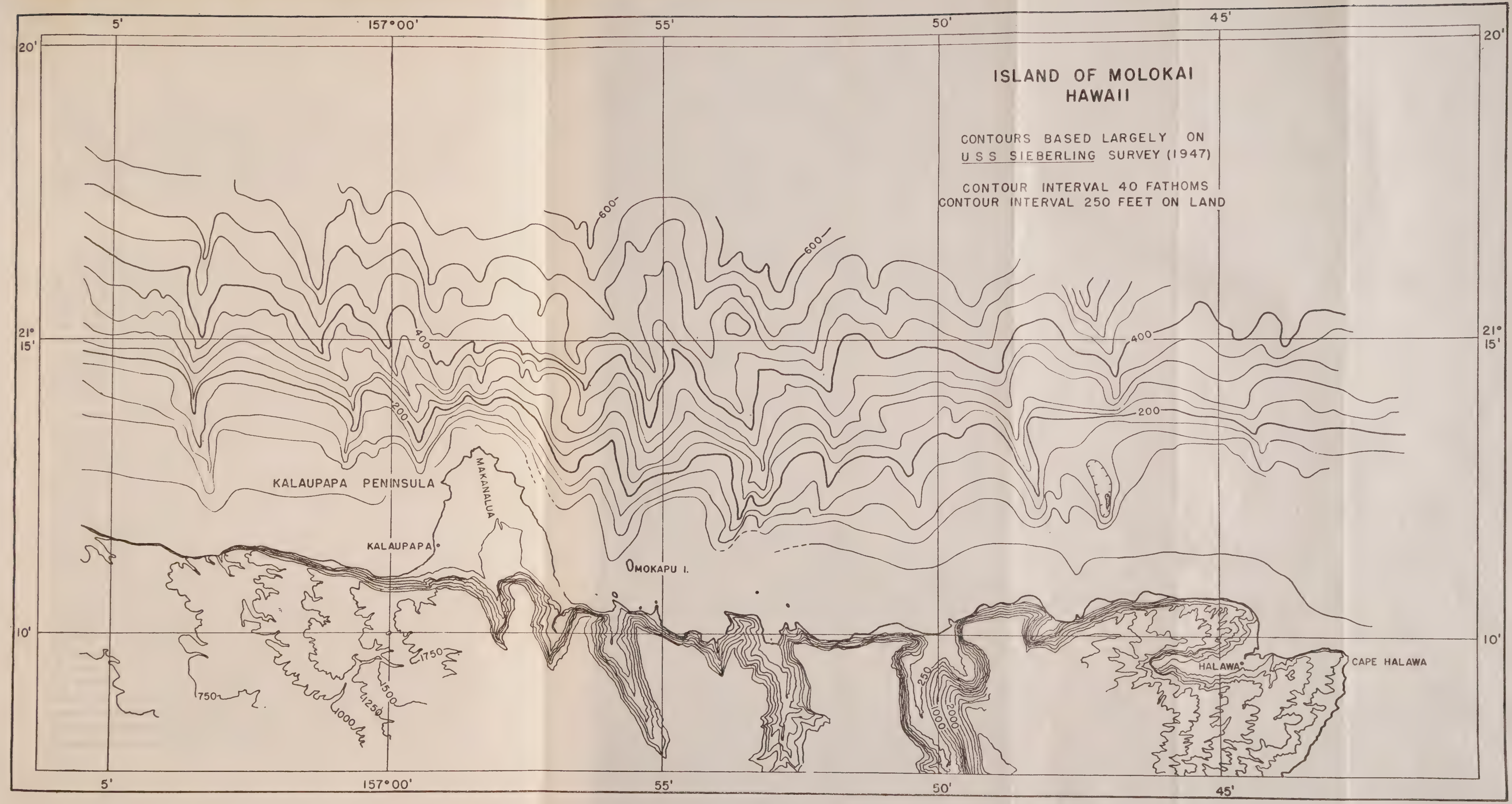
5'
157°00'
55'
50'
45'
20'
21°
15'
10'
ISLAND OF MOLOKAI
HAWAII
CONTOURS BASED LARGELY ON
USS SIEBERLING SURVEY (1947)
CONTOUR INTERVAL 40 FATHOMS
CONTOUR INTERVAL 250 FEET ON LAND
600
600
400
400
200
200
KALAUPAPA PENINSULA
MAKANALUA
KALAUPAPA
OMOKAPU I.
HALAWA
CAPE HALAWA
750
1000
1250
1500
1750
250
1000
2000

Figure 4. The submarine canyons north of Molokai, Hawaiian Islands. Note relation of sea and land canyons.

would have insufficient gradients for landslides to dispose of the fill. This universality of canyons suggested the possibility that the cause of the canyon cutting and submergence was a change in sea level rather than a world-wide movement of the crust. If this change has taken place, it should be registered in other ways. The rest of this paper will deal accordingly with other lines of evidence.

CORAL REEFS

The suggestion of wide scale submergence came from coral reef studies at an even earlier date than from the submarine canyons. As is well known, reef corals grow only at shallow depths. Darwin (1842) first proposed that the atolls represented the growth of coral masses on top of submerging volcanoes. This idea has been as hotly disputed as has the stream origin of canyons. Foremost among the contending hypotheses has been that of Daly (1910). He suggested that wave planation of island tops occurred during low stands of the sea accompanying high latitude glacial stages. He attributed the atolls to the growth of coral crescents around the rims of the levelled platforms during the rising sea level accompanying glacial melting.

Fortunately, it has been possible to apply fairly conclusive tests to these two contending hypotheses. If the wave planation idea is correct, one would expect that boring into the atolls would expose the wave abraded platform at moderate depths. On the other hand, the Darwin hypothesis would be supported by finding shallow water formations extending to great depths. We are now in possession of evidence from four borings into atolls at scattered points in the western Pacific. All of them show the same result, namely, that no wave abraded platform was discovered. The recent boring on Bikini (Ladd, Tracey, and Lill, 1948) provides the best evidence. It extended to 2,500 feet and shows, so far as has been found, nothing but shallow water formations for the entire depth. The core is in no way indicative of being talus material later grown over by an advancing reef, as Daly has contended. The boring partially confirms the geophysical evidence which suggests that the igneous core is from 6,000 to 13,000 feet below the surface (Dobrin, *et al.*. 1946). Another relatively recent boring on an atoll northeast of Borneo (Kuenen, 1947) revealed deposits of coral limestone and lagoonal marl down to a depth of 429 meters, the bottom of the hole. Relative to a somewhat earlier drilling on the former Japanese island of North Borodino, a slightly elevated atoll east of Okinawa, the Japanese (Hanzawa, 1940) reported 431 meters penetration through calcareous sand and limestone with shallow water foraminifera along the entire length. The earliest and best known of the cores was from the atoll of Funafuti. According to what is known of this core, the entire 1,114 feet is indicative of shallow water origin and of materials like those of the present reef or of the lagoon. The investigation of the core was made so long ago that the results are now questioned. Some of the core is to be restudied in the near future to bring the data into line with what is now known about ecology of organisms.

Indications of submergence are less pronounced in the case of the borings of the Queensland Reef off the Australian coast (Richards and Hill, 1942). Here the reef proves to have a thickness of only about 400 feet. It does not overlie a wave-abraded platform but rests on a coarse grit formation suggestive of shallow water deposition. At Bermuda the borings revealed weathered rock at 245 feet, sand and gravel at greater depths, and finally volcanic material at 560 feet, but no definite wave-cut platform. The results of the deep borings in the Bahamas by oil companies are not yet published, but it is known that they have penetrated some 14,000 feet of limestone, all apparently of shallow water origin.

According to Kuenen (1933), evidence of submergence of the coral islands comes from the steep slopes which surround some of them. These slopes are considered too steep for talus and are interpreted as due to upgrowth as the reefs submerged. Also, Kuenen has called attention to the existence of atolls rising from deep platforms which have no evidence of vulcanism, so that the atolls have evidently grown up as the platforms submerged. Davis (1928) introduced various other lines of evidence, too numerous to list, suggesting submergence of the coral islands. Perhaps the most impressive of these is the wide distribution of atolls in the central Pacific in areas where remnants of volcanic islands are not found (Fig. 5). It would be most surprising if volcanic islands, many of which must have been as large as the Hawaiian group, have been so completely bevelled by the waves as to leave nothing but platforms. Obviously, this abrasion could not be accomplished during short glacial epochs. Furthermore, if reefs have simply grown on the tops of shallow banks, it is difficult to account for the absence of an equal number of shallow reefless banks in the zones north and south of the coral seas.

Age of Submergence. The time of submergence of the coral islands may not be the same as that of the submarine canyons. The Bikini boring has shown definitely that there are Tertiary formations at depths of 900 feet or less. Pliocene is underlain in turn by Miocene. Similarly, the deep Bahama boring passes down through most of the Tertiary. These borings suggest a gradual submergence and by them-

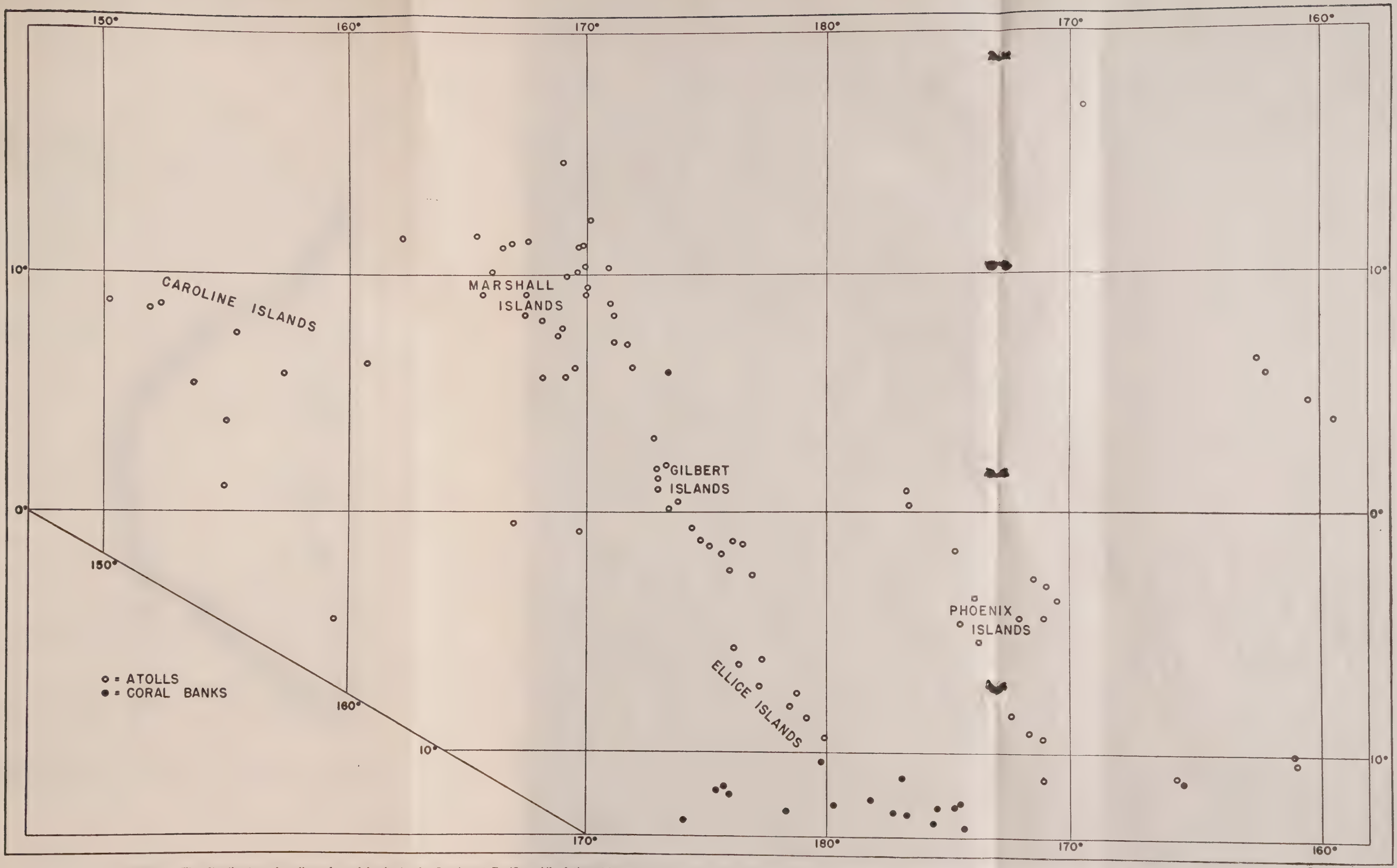
150°
160°
170°
180°
170°
160°
10°
0°
CAROLINE ISLANDS
MARSHALL ISLANDS
GILBERT ISLANDS
ELLICE ISLANDS
PHOENIX ISLANDS
○ = ATOLLS
● = CORAL BANKS

Figure 5. The distribution of atolls and coral banks in the Southwest Pacific. All of these islands lack volcanic rocks so far as is known, and except in the Caroline Islands volcanic islands are missing from these groups.

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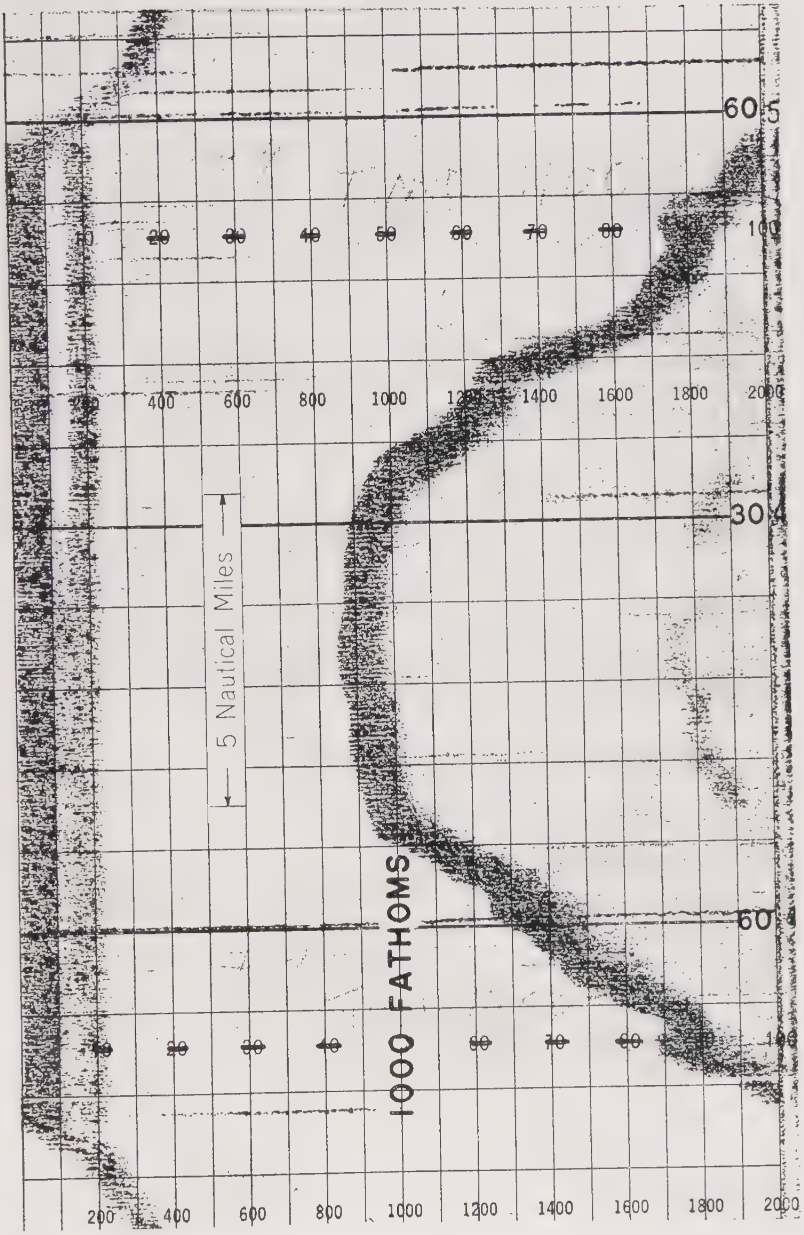

Figure 6. A fathogram of a seamount with terraces in the Gulf of Alaska. Center of seamount is at Lat. 52° 34′ N, Long. 151° 19′ W.

selves are not indicative of sea level changes. The deep Funafuti boring was apparently all in Pleistocene and may be contemporaneous with and related to the Pleistocene portions of the canyons.

FLAT-TOPPED SEAMOUNTS (GUYOTS)

An interesting discovery came from the use of the recording echo sounding devices by the Navy during World War II. A series of flat-topped, deeply submerged mountains was found in the West Central Pacific. We are indebted to Hess (1946) for most of the available information on these bevelled mountains, which he has termed "guyots." The flat tops were found to vary considerably in level, but about 50 per cent of those in the Southwest Pacific lie close to 800 fathoms in depth. On the other hand, the seamounts in the Gulf of Alaska and off the California Coast have summit flats at variable depths averaging around 400 fathoms.

The seamounts off California have terraces. The same appears to be true of the submerged mountains in the Gulf of Alaska (Fig. 6). Both the terraces and the flat tops are difficult to explain except as wave-bevelled platforms, or in the West Central Pacific as submerged coral banks. In either case the surfaces must have been brought close to sea level so that we appear to have further evidence of large submergence. Some flat-topped mountains were discovered in recent work by Maurice Ewing in the Atlantic. It should be pointed out, however, that in the Antarctic R. S. Dietz obtained fathograms during the 1946–1947 expedition and failed to find any flat tops to the mountains or ridges which he discovered. Probably information will become available soon from many other areas.

Information concerning the materials of the seamounts was obtained in a recent cruise of the Navy Electronics Laboratory vessel EPCE(R) 857. During this cruise Twin and Erben Banks, 580 and 860 miles off southern California, were explored under the direction of R. S. Dietz. Dredgings procured volcanic rocks with rounded cobbles from each bank at depths of about 350 fathoms. On Erben Bank the cobbles were embedded in a crust of manganese which had a thickness of 4 cm. If Pettersson's (1945) estimate of the rate of radial growth of manganese nodules of 1 mm/1,000 years is correct, the suggestion is that Erben Bank has been submerged about 40,000 years. This, of course, assumes that manganese accretion began as soon as the bank became deeply submerged, which may not have been the case. Indirect evidence of the age of guyots in the Marshall Island area comes from the boring at Bikini. The atoll appears to be built on one edge of a guyot platform, so that the flat top of the seamount could be considered as older than the formations which cover it. Since the 2,500 foot drilling has penetrated to Lower Miocene, the guyot surface is apparently pre-Miocene. Hess (1946) suggested that the guyots of the Southwest Pacific were bevelled in the pre-Cambrian and that they have been sinking slowly ever since due to oceanic sedimentation which has weighed down the floor of the ocean. This is an interesting suggestion, but seems rather unlikely in view of other evidence of what must be much more recent submergence.

COARSE SEDIMENTS AND SHALLOW WATER FORMS OBTAINED FROM GREAT DEPTHS

Geologists have generally assumed that coarse detrital sediments could be deposited only in shallow water, although it was recognized that some coarse material could be transported to a deep water environment by rafting or even by landsliding. Rafted sediment dropped into deep water can usually be distinguished by the finding of coarse debris mixed with typical deep-water deposits. Landslide deposits are largely confined to the base of relatively steep slopes, but they are otherwise not easy to distinguish in bottom samples. In general, one might expect to find coarse debris mixed with sediments in the vicinity of great glaciers discharging into the oceans, as, for example, around Antarctica and Greenland. Such finds have been numerous and the deposits are called "glacial marine." However, the finding of coarse sediment in deep water at considerable distance from the ice fronts should be rare because of the limited amount of transporting facilities other than icebergs. The debris drifted by vegetation mats, tree trunks, and kelp must constitute an insignificant proportion of the deep sea sediment which is contributed by marine life and colloidal material carried from land by currents. Therefore, it is interesting to find that coarse sediments are not uncommon among the few ocean cores now available. Sand layers have been obtained in cores from the deep Atlantic far from any shoal areas, according to H. C. Stetson and Maurice Ewing. Cross-bedded sand was found in the Gulf of Mexico at over 2,000 fathoms according to Trask, Phleger and Stetson (1947). According to R. Revelle, cores obtained by Scripps Institution in the deep basins off California and Lower California have also shown sand layers. Gravel was found in the Dutch East Indies at 20 out of 385 stations, in depths ranging from 192 to 1,400 fathoms (Neeb, 1943: table 2 on pp. 72–85, also 225–227). It is possible that this coarse material was deposited at great depth, but the alternative of submergence must be considered.

Other evidence comes from the rounded nature of the rocks dredged from ridges and seamounts. Since the violent turbulence of shallow water conditions is necessary to produce rounding, rocks formed on the deep ocean floor by vulcanism would rarely, if ever, be rounded. Some of the rounded rock obtained in the North Atlantic may have been introduced by ice, but the cobbles on banks and seamounts off California (Shepard, 1941: 1869, pl. I) are in all probability an indication of submergence. It is unfortunate that so few of the marine highs have been sampled, but it is probably significant that a large per cent of those which have been explored have yielded rounded rocks. If the percentage holds good for future exploration, this source of information will add substantial evidence to the other lines. Possible confirmation of the rounded rocks in dredgings comes from the numerous chart notations of gravel in deep water.

The coring operations under the direction of Pettersson (1946) in the Mediterranean yielded evidence that the deep parts of that sea may have been shallow at not too remote a period. The cores contained layers with abundant molluscs, the latter being almost entirely confined to a shallow water habitat. Dangeard (1928) reported the discovery of lamellibranch shells with gastropod borings in 660 fathoms west of the Strait of Gibraltar. Beebe (1932: 39) reported a dredging of shallow water shells along with rounded gravel at 1,200 fathoms on a ridge off Bermuda. Kuenen (1933) referred to the dredging of recent coral reef material in 550 fathoms in the Ceram Sea. Of possible less significance was the discovery of littoral shells at depths of 1,420 fathoms off the Norwegian Coast (Hull, 1912). Much more exploration is required before the faunal evidence can be properly evaluated.

INSULAR FAUNAS AND FLORAS

The submergences indicated by the preceding lines of evidence should be reflected also in the faunas and floras of islands, provided that the submergences had been of sufficient extent to destroy former land bridges to the mainland or to adjacent islands. The literature relative to island connections is large and some of it contradictory. Some extremists claim former connections of many of the true oceanic islands with the mainland, but the general concensus of opinion seems to be that islands separated from the mainland by deep and wide channels, that is, channels over 1,000 fathoms deep and 100 miles or more in width, have waif faunas and floras, either rafted to or blown onto the islands. On the other hand, the life forms of islands on the continental shelves are for the most part clearly related to the adjacent continents and require land bridges.

Between the extremes of true oceanic islands and continental shelf islands are the cases where there are channels of depths between 100 and 1,000 fathoms. Among the best known of this group are the islands of the "continental borderland"[2] off southern California. Here the sills of the channels range from 150 to 450 fathoms. The faunas of all of the larger of these islands include endemic species which are difficult to explain without land bridges. The presence of endemic foxes is particularly impressive, since it seems impossible that these animals could drift on a log for the forty miles or more required for transportation to the outer islands. The Pleistocene elephants of Santa Cruz Island are undoubted evidence of a former land connection at this place.

The fringing islands of the West and East Indies and of such groups as Madeira and Cape Verde Islands of the Atlantic have separations of intermediate depths, and like the California islands have faunal evidence of former connections. Extensive bibliographies cover this subject but the evidence is not entirely conclusive.

SUMMARY AND CONCLUSIONS

An examination of available information from the sea floor around the continents and around oceanic islands provides abundant evidence of large scale submergence. The investigation of submarine canyons has now yielded so much indication of subaerial origin that the world-wide distribution of these features constitutes the most conclusive evidence that the continental margins and even some of the oceanic islands once stood thousands of feet higher in relation to sea level than they do at the present time. Widespread submergence of oceanic islands in the coral island areas, long ago advocated by Darwin, has now been well confirmed by recent borings in widely separated places. This evidence indicates that extensive tracts of the ocean floor have been considerably depressed. The recent discoveries of flat platforms on the tops of deep seamounts suggest a former elevated condition during which waves bevelled the platforms to sea level, or that the flat surface was developed at sea level by calcareous reef builders. Evidence from bottom samples is somewhat less conclusive than that of the canyons and coral islands, but the limited dredgings and corings available from deep water contain a large per cent which have evidence of former shallow-water conditions. Insular faunas in general are also of a character which favors considerable submergence, particularly along the continental margins. The deep fills in many of the mouths of river valleys, not discussed here, are still further evidence in the same direction.

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[2] A term referring to broad submerged areas seaward of and deeper than the continental shelves but landward of the principal continental slope.

The significance of all of these converging lines of evidence in the unravelling of the late geological history should be profound. Unless further exploration provides very different evidence from that which is now available, we shall be forced to conclude that the continental margins and the islands have undergone great submergence alike in areas where stability was supposed to have long prevailed and in areas where other lines of evidence indicate either great crustal rising (as along much of the California Coast) or long-continued crustal submergence (as at the delta of the Mississippi). The world-wide nature of the evidence suggests a change of sea level, and the indication of Pleistocene origin of at least some of the submarine canyons could be used as an indication that the changing sea level resulted from the extraction of water during glaciation. However, the extent to which the sea could be lowered by this means is most difficult to determine. The common estimates of 40 fathoms may be far too small (Shepard and Emery, 1941: 146–155), since the ice could have been much thicker on the continents than generally assumed and may have covered much more territory than is considered in the usual estimates, particularly in the Arctic and along the continental margins. On the other hand, some of the recent evidence indicates that the submergence, at least of the coral reef islands, was going on all through the Tertiary. Possibly the same may be true of the submarine canyons, and the evidence of Pleistocene origin now available may apply only to the upper near-shore portions where glacially-controlled sea levels may have been important factors. However, the failure to find breaks in the canyons between any apparent Pleistocene excavation and canyons of earlier age is disconcerting. None of the well-explored canyons which can be traced into shallow water show a change in character at a depth of the order of 40 fathoms (the supposed glacial low sea level), nor has any other depth down to about 1,000 fathoms shown any indication of such a change.

In conclusion we are confronted with abundant evidence of world-wide submergence, some of it Pleistocene and some Tertiary or even earlier. It is time that these facts be faced by those geologists who have been trying to hold back the tide. More exploration is badly needed, but new hypotheses should utilize the wealth of oceanographic data now available.

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Contribution No. 388

SULFATE-REDUCING BACTERIA IN MARINE SEDIMENTS[1]

By

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The occurrence of hydrogen sulfide in the waters of certain seas, fjords, and basins, as well as the presence of black or "blue" stinking sediments, can hardly escape the notice of any marine scientist. It is not surprising, therefore, that the eminent oceanographer Murray (Murray and Irvine, 1895) concerned himself with the nature of these materials and postulated their bacterial origin even before bacteriologists had described the specific organisms involved.

It is now accepted that much of the sulfide arises from the bacterial reduction of sulfate. Bacteria which reduce sulfate appear to be very widely distributed in the sea, and it is the purpose of this report to summarize our knowledge of these bacteria with particular reference to their significance in marine sediments, a subject which has been under investigation for several years by the authors and their collaborators at the Scripps Institution.

NOMENCLATURE

Virtually all bacteria and higher plants, as well as a good many animals, may reduce the sulfur in sulfate to the sulfhydryl or disulfide form in the process of synthesizing sulfur-containing proteins, but the term "sulfate reducer" is applied only to those organisms which can utilize sulfates as hydrogen acceptors in their energy-producing reactions. The sulfur in excess of that required for the synthesis of protoplasm is generally reduced to and liberated as hydrogen sulfide by such organisms. As far as is known, only a limited group of bacteria has this unique property. Most of the common bacteria, yeasts, and molds which have been reported to produce traces of hydrogen sulfide from sulfate probably do so by the synthesis of sulfur-

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containing proteins which, upon the death and autolysis of the cells, are decomposed with the liberation of hydrogen sulfide. The amount of sulfate so reduced to hydrogen sulfide by this process, called "indirect reduction" by Beyjerinck (1900), is extremely small compared to the large amounts reduced to hydrogen sulfide by the true sulfate-reducing bacteria.

Although there were earlier reports of the microbial reduction of sulfate to hydrogen sulfide, Beyjerinck (1895) is credited with the isolation of the first pure culture of a sulfate reducer originally called *Spirillum desulfuricans,* which was found in ditch water at Delft, Holland. A similar organism, designated *Microspira aestuarii,* which required three per cent salt for its growth, was isolated from mud and water along the North Sea coast by van Delden (1904). A third sulfate-reducing organism called *Vibrio thermodesulfuricans,* allegedly differing from the two named above only in having a higher optimum temperature for growth, was described by Elion (1924).

Baars (1930) regarded all three organisms as varieties of a single species, which he termed *Vibrio desulfuricans,* since he found that certain fresh-water, salt-water, and thermophilic cultures were interconvertible by laboratory acclimatization procedures. These observations were substantiated by Starkey (1938), who also showed that his cultures could be induced to form endospores. He, therefore, proposed the generic name *Sporovibrio* for the entire group of sulfate reducers.

Rittenberg (1941) was unsuccessful in repeated attempts to induce the cultures of sulfate reducers isolated from marine sediments to form spores. Neither could they be adapted to grow in fresh-water media nor at temperatures higher than 40° to 45° C. These observations suggest that at least some of the sulfate reducers found in the sea are sufficiently distinctive to be considered as separate species.

For reasons outlined by the senior author in Bergey's (1948) Manual, it seems best to apply the generic name *Desulfovibrio* to the entire group of sulfate-reducing vibrios, and *Desulfovibrio aestuarii* to the marine forms. Besides *Desulfovibrio aestuarii,* which seems to be quite widely distributed in the sea, there may be several other related species of sulfate reducers in recent or ancient marine sediments and possibly other genera with similar physiology, but information in this regard is too fragmentary for valid conclusions.

MORPHOLOGY

The characteristic form of *Desulfovibrio aestuarii* in young, actively reproducing cultures is that of a slightly twisted spirillum or curved rod ranging in size from 0.6 to 0.8 μ in width by 3 to 4 μ in length.

The young cells may occur in chains of four or more cells attached end to end by plasmodesm, giving such groupings of comma-shaped rods the appearance of long spirilla. Coccus forms and straight rods also occur under certain conditions in young cultures. Older cells may be highly pleomorphic with coccoid forms, rods with swollen ends, and other bizarre forms predominating. Metachromatic granules (probably volutin), sulfur granules, and deposits of iron sulfide have been observed in cells. Beyjerinck (1895), Issatschenko (1929), Baars (1930), and others have noted marked thickenings of older cells or dead cells due to the accumulation of iron sulfide.

While there may be species peculiarities, the morphological variations are attributable primarily to the conditions under which the bacteria have been cultured. The chemical composition, osmotic pressure, pH, and oxygen tension of the medium influence the morphology of sulfate reducers.

In the absence of free oxygen, most young cells are actively motile by means of one or more flagella. Electron microscope photographs of *Desulfovibrio aestuarii* show that these marine species have a single flagellum which generally has a polar insertion. Starkey (1938) found that his sporogenous cultures had peritrichous flagella, the number and location being quite variable.

The *Desulfovibrio* stain fairly well with the common aniline dyes. They are Gram negative.

PHYSIOLOGY

Sulfate reducers are obligate anaerobes. Though not killed rapidly by exposure to oxygen, they fail to reproduce in the presence of free oxygen. Growth is best in a reducing medium, an oxidation-reduction potential of E_h − 0.1 to − 0.3 volt at pH 7 and 30° C being most favorable for multiplication. In asparagine lactate medium, the first evidence of sulfate reduction observed by Aleshina (1938) was at E_h + 0.027 volt. As sulfate reduction proceeded, the oxidation-reduction potential of the medium dropped to E_h − 0.2 to − 0.3 volt, at which point conditions were optimal. The sulfate reducers studied by Starkey and Wight (1945) grew within the range of pH 5.5 to 8.5 and reduced the E_h from + 0.3 volt to − 0.2 or − 0.3 volt. The pH range of the marine species is 5.4 to 9.0, the optimum being pH 6 to 8.

Under favorable conditions certain cultures may produce as much as 1,500 mgm/L. of hydrogen sulfide. According to Baars (1930), halophilic strains produce considerably more hydrogen sulfide than fresh-water strains—his cultures of the former producing a maximum of 1,448 mgm/L. as compared with only 794 mgm/L. for the latter. Rittenberg (1941) found that the rate and the total amount of hydrogen sulfide produced by *Desulfovibrio aestuarii* varied with the concentration of salt in the medium. In general, increasing the salt content within the range of 2 to 4% diminished the rate but increased the total amount of hydrogen sulfide produced. This may be illustrated by the following results:

Period of incubation	*Hydrogen sulfide formed in media containing* 2% NaCl	3% NaCl	4% NaCl
119 hours	56 mgm/L.	37 mgm/L.	8 mgm/L.
143 hours	370 mgm/L.	234 mgm/L.	30 mgm/L.
167 hours	520 mgm/L.	513 mgm/L.	126 mgm/L.
191 hours	622 mgm/L.	660 mgm/L.	518 mgm/L.
239 hours	692 mgm/L.	809 mgm/L.	902 mgm/L.
287 hours	715 mgm/L.	826 mgm/L.	1013 mgm/L.

Sulfur, sulfite, thiosulfate, and tetrathionate are also reduced to hydrogen sulfide by sulfate reducing bacteria. These compounds are assumed to be intermediates in the reduction of sulfate and are assumed to be reduced more readily than sulfate, since they do not accumulate in the medium.

It is a moot question whether sulfate is ever reduced only to and deposited as sulfur in an anaerobic environment, although recently Datta (1943) described an organism as a new species which was claimed to have this ability. Sulfur is often found in cultures or cells of sulfate-reducing bacteria, but there is always some question as to whether it is formed directly from the reduction of sulfate or from the oxidation of sulfide upon coming into contact with oxygen or other oxidizing agents. It is possible, as suggested by Zil'berman (1940), that sulfite, which is believed to be an intermediate product in the reduction of sulfate, reacts with hydrogen sulfide to produce free sulfur: $H_2SO_3 + 2H_2S \rightarrow 3S + 3H_2O$

Apart from sulfate and the intermediate inorganic sulfur compounds already mentioned, no other hydrogen acceptors have been demonstrated for this group of bacteria. Several organic sulfur compounds, phosphate, selenate, tellurate, and peptone were tested in this connection (Rittenberg, 1941) with negative results. Nitrate, although assimilated as a source of nitrogen, was not utilized as a hydrogen acceptor in the energy-yielding reactions of the sulfate reducers.

There are strains of sulfate-reducing bacteria which can utilize nearly any type of organic matter as hydrogen donors. Energy can apparently be derived by sulfate reduction and the concomitant oxidation of cellulose (Rubentschik, 1928), chitin and glucosamine (Aleshina, 1938), beef and mutton tallow (Seliber, 1928, 1945), aliphatic and aromatic hydrocarbons (Rosenfeld, 1947), and other resistant materials.

Simple compounds like lactate and asparagine are the best sources of carbon or energy for most cultures of sulfate-reducing bacteria. A large variety of mono- and disaccharides, alcohols, aldehydes, aliphatic acids, and amino acids are metabolized by some species.

The types of materials used vary somewhat from strain to strain. Baars (1930) described *Desulfovibrio rubentschikii* as a new species of sulfate reducer primarily upon a basis of its ability to attack fatty acids and sugars not used by other species.

HYDROGEN UTILIZATION

A large body of data indicate that at least certain sulfate reducers can obtain energy by the oxidation of molecular hydrogen and even live autotrophically by this mechanism. The work of Nikitinsky (1907), Kroulik (1913), and Niklewski (1914) gave presumptive evidence of hydrogen uptake by sulfate reducers, but it remained for Stephenson and Stickland (1931) to isolate, from river mud, a pure culture which reduced sulfate to hydrogen sulfide with the consumption of molecular hydrogen:

$$H_2SO_4 + 4H_2 \rightarrow H_2S + 4H_2O + 56{,}750 \text{ calories.}$$

This culture, designated Strain 182, also catalyzed the reduction of sulfite and thiosulfate with molecular hydrogen. The demonstration of hydrogen uptake was obtained with resting cells using the Warburg technique, and there was no proof of carbon dioxide uptake or cell synthesis under these conditions. Wight and Starkey (1945), however, demonstrated the ability of sulfate reducers to live autotrophically by obtaining their energy requirements from the oxidation of molecular hydrogen and their carbon from bicarbonate or carbon dioxide. Certain other cultures studied by Starkey and Wight (1945) utilized hydrogen in lactate medium but not in a purely mineral medium.

Several different pure or partially purified cultures of sulfate-reducing bacteria, isolated from marine mud, were reported by ZoBell (1947a) to consume hydrogen while producing hydrogen sulfide from sulfate in a strictly mineral medium. The ratio of the amount of hydrogen consumed to the amount of hydrogen sulfide produced exceeded the theoretical value of 4.0 which would result if hydrogen were oxidized quantitatively to hydrogen sulfide and water. This suggests that part of the hydrogen may have been used to reduce carbon dioxide in the synthesis of cell substance.

OTHER CULTURAL REQUIREMENTS

Considerable importance has been attached to the salinity requirements of sulfate-reducing bacteria, because this has been employed as the main criterion for distinguishing the marine or halophilic species, *Desulfovibrio aestuarii*, from other species. Baars (1930) was able to acclimatize a fresh-water strain to grow in a medium containing 3% salt, and therefore he concluded that the strains were identical. It should be pointed out that the fresh-water culture Baars employed produced some hydrogen sulfide in his 3% salt medium before the adaptation procedure. In this instance at least "adaptation" may have been a selection process. Rittenberg (1941), however, could not induce halophilic strains which he isolated from marine sediments to grow in nutrient fresh-water medium. They grew normally, though with decreased sulfide production, when the sea water medium, in which they were most active, was diluted 1 : 1 with fresh-water medium. A few cultures were induced to grow in a nutrient medium containing only 25 parts of sea water to 75 parts of fresh water, but only a little hydrogen sulfide was produced. The lack of adaptability was also reflected in the abnormal morphology of the sulfate reducers which were induced to grow in media containing less than 50% sea water.

The salinity picture is further complicated by the observations of other investigators. Strains apparently indistinguishable from *Desulfovibrio desulfuricans* and *Desulfovibrio aestuarii* in all other respects have been described with a salt optimum of 8% and a growth range between traces and 20% sodium chloride (Chait, 1924); with an optimum of 5% (Rubentschik, 1928); with salt ranges of traces to 1%, traces to 5%, and 1% to 3% (Gahl and Anderson, 1928); with a range of 1% to 18% (Ginsburg-Karagitscheva, 1933); and so on. It is entirely possible that there are obligate halophiles, obligate fresh-water strains, and a host of intermediate forms with varying ranges of salt tolerances. Any attempt to classify these various forms into separate species, however, should logically wait until some knowledge is obtained concerning the mechanism of salt adaptation and the factors controlling the salt ranges of growth.

Similarly, various temperature ranges and optima have been reported for different cultures of sulfate-reducing bacteria. His being able to develop cultures, from the same material, having an optimum temperature of either 30° or 55° C., led Baars (1930) to regard Beyjerinck's (1895) *desulfuricans* (optimum temperature of 30°) and Elion's (1924) *thermodesulfuricans* (optimum temperature of 55°) as adaptation forms of the same plurivalent or thermally adaptable type. However, since Baars did not start with single cell isolations, he may have been producing enrichment cultures of one type or the other of organisms of different potentialities initially present by the selective temperature of incubation. Rittenberg (1941) was unable to acclimatize pure cultures of *Desulfovibrio aestuarii* isolated from marine sediments to reduce sulfate at temperatures higher than 40° to 45° C.

OCCURRENCE IN THE SEA

Sulfate-reducing bacteria appear to be abundantly and widely distributed in the marine environment, especially in bottom deposits. Such bacteria are occasionally found in samples of sea water, where their presence may be of doubtful significance, since sulfate reducers are active only in strictly anaerobic environments. In the wake of a prolific diatom bloom or other circumstances resulting in the occurrence of enough decaying organic matter to consume all of the dissolved oxygen, or in stagnant water basins, conditions in sea water may be suitable for the activity of sulfate reducers. Such conditions prevail in the Black Sea, the water of which contains no free oxygen at depths exceeding 200 meters (Sverdrup, *et al.*, 1942). Water below the euphotic zone in the Caspian Sea, Norwegian fjords, and certain localized areas in the ocean are also sufficiently anaerobic at times to favor the growth of sulfate reducers. The activities of sulfate reducers are largely responsible for maintaining anaerobic conditions by the production of hydrogen sulfide which depletes free oxygen.

According to Daniltchenko and Tschigirine (1926), the concentration of hydrogen sulfide near the bottom of the Black Sea, where sulfate reducers are most active, is sometimes as high as 3,000 mgm/L. Copenhagen (1934) described an area approximately 25 by 200 miles in the Atlantic Ocean off Walvis Bay, South Africa, where hydrogen sulfide is produced periodically by sulfate reducers in quantities sufficient to be lethal to flora and fauna almost to the surface of the overlying water.

It was in the Black Sea where sulfate-reducing bacteria were first demonstrated by Zelinski (1893). Issatschenko (1924, 1929) and Ravich-Sherbo (1930) found vigorous sulfate reducers in virtually all Black Sea water samples examined. In the Caspian Sea, Butkevich (1938) found up to two million bacteria per ml. of water, many of which were sulfate reducers. Sulfate reducers were found in the Salton Sea by Brannon (1914), in the Mediterranean Sea by Bertel (1935), and in Russian limans by Rubentschik (1928). The freshening of certain limans in the Odessa region during the rainy season was found by Rubentschik and Goicherman (1936) to be followed by a ten- to thousand-fold increase in the abundance of sulfate reducers.

In bottom deposits, where bacteria are generally most abundant, ZoBell (1938) demonstrated from 1,000 to 10,000 sulfate reducers per gram. Large numbers of sulfate reducers were found by Bavendamm (1932) in nearly all samples of calcareous mud in the region of the Bahama Islands. A good many of the bacteria recovered from deep sea bottom deposits by Ginsburg-Karagitschewa and Rodionowa (1935) were sulfate reducers.

Rittenberg (1941) found viable sulfate reducers in about half of 450 2- to 3-gram samples (wet weight) from 160 different stations off the coast of California and Lower California. Profile series showed that the abundance decreased with the depth of the sediment, sulfate reducers being detected in only 10% of the samples from depths exceeding 60 inches, as compared with 32% positive at depths of 12 to 60 inches, and 64% positive in the topmost 12 inches of sediment. Sulfate reducers were detected in 92% of the samples of silty sand, 86% of the sandy silt samples, 65% of the silty mud samples, and in 51% of the samples of clayey mud.

The presence of these bacteria, together with the occurrence of sulfide and the decreasing concentration of sulfate with depth in the interstitial water in certain sediments, suggests that the sulfate reducers have been active *in situ*.

OCCURRENCE IN ANCIENT MARINE SEDIMENTS

Bastin (1926) demonstrated the presence of sulfate-reducing bacteria in 28 oil-field waters, believed to have a marine origin, out of 30 sampled in Illinois and in 15 out of 37 sampled in California. He attributed the generally low content of sulfate in oil-well waters to the activity of the bacteria. The samples of oil-well waters were obtained from ancient marine sediments at depths ranging from 400 to 1,866 feet. Similar observations were made by Gahl and Anderson (1928), who found sulfate reducers in 17 out of 40 oil-well waters sampled in California fields from depths as great as 3,090 feet. The isolated organisms grew at temperatures ranging from 28° to 50° C. The temperature of the oil-well waters was 44° to 47° C.

Sulfate reducers were found in the water from six producing oil wells in Illinois fields by Bastin and Greer (1930). The waters were rich in hydrogen sulfide. In oil-well waters containing no sulfide, sulfate reducers were absent. Further evidence that sulfate-reducing bacteria are present and active in waters associated with petroleum deposits has been presented by Ginter (1930, 1934). He points out that carbonate and sulfide in many brines increased as sulfate decreased, presumably due to the reduction of sulfate to hydrogen sulfide and the simultaneous oxidation of carbon compounds to carbon dioxide which appears as carbonate or bicarbonate.

Besides demonstrating the occurrence of sulfate reducers in water from several oil wells, Ginsburg-Karagitscheva (1933) reported the presence of such bacteria in 14 out of 15 samples of oil sands from Grozny oil-field formation. The bacteria were believed to be indigenous species responsible for the abundance of hydrogen sulfide, the low concentration or lack of sulfate, and the modification of the associated crude oil. Baier (1937) reasoned that sulfate reducers could be active at the oil-water interface where petroleum constituents provide the carbon and energy necessary for the growth of the bacteria.

While the possibilities of surface contamination have not been ruled out, it is significant that sulfate reducers are generally the predominant bacteria detected in oil-well waters. They grow best or exclusively at the temperature and salinity of the water in which they were found, and it has been established that the sulfate reducers can obtain all of their food requirements from the reservoir fluids in which they are found. This circumstantial evidence, plus the fact that appreciable numbers of sulfate reducers have been recovered from oil wells long after anything has been introduced into the wells, strongly suggests that if the bacteria are not actually species indigenous to the formation, they have been multiplying in the oil wells.

ZoBell (1946) detected living sulfate-reducing bacteria in aseptically collected samples of sulfur limestone anhydrite from a depth of 1,560 feet. Cultures which reduced sulfate at temperatures ranging from 75° to 85° C have been observed. Recent observations indicate that the activity of sulfate reducing bacteria is promoted by high hydrostatic pressures such as prevail in the ocean or in petroleum deposits at depths of several thousand feet.

IMPORTANCE OF SULFATE REDUCERS IN SEDIMENTS

There are several ways in which the activities of sulfate-reducing bacteria may modify conditions in marine sediments both recent and ancient. Besides contributing to the sulfur cycle in sediments (Galliher, 1933) by converting sulfate into sulfide and possibly to free sulfur, they transform various kinds of organic matter, consume molecular hydrogen, affect the pH and E_h of their environment, and otherwise influence chemical or physico-chemical conditions.

The free sulfur quite commonly found by Buchanan (1891) in marine bottom deposits was believed to result from sulfides coming in contact with oxygen in the overlying water. He was mistaken, though, in believing that sulfate was reduced to sulfide by the digestive secretions of animals. Hunt (1915) has attributed the origin of sulfur deposits in Sicily to the bacterial reduction of sulfate, and the Louisiana and Texas Gulf Coast sulfur deposits were believed by Ridgway (1930) to result from the bacterial reduction of gypsum. Ahlfeld (1937), Murzaiev (1937), and Sturm (1937) agree that certain sulfur deposits in Russia resulted from the oxidation of hydrogen sulfide that could have come only from the bacterial reduction of sulfate. Associated with sulfur deposits on the east coast of India, Iya and Sreenivasaya (1945 a, b) found sulfate-reducing bacteria which were thought to form sulfur.

Sulfate reducers may quite definitely contribute to the formation of metallic sulfide deposits. Murray and Irvine (1895) attributed the formation of ferrous sulfide deposits in black marine mud to the activity of sulfate-reducing bacteria, which were also believed to account for the loss of sulfate and an increase in the carbonate content, the latter resulting from the oxidation of organic matter by bacteria. The increased carbonate content in the mud examined on the CHALLENGER Expedition was equivalent to the decreased sulfate content.

Issatschenko (1929) demonstrated the formation of iron sulfide inside the cells of sulfate-reducing bacteria, which were credited with being responsible for the deposition of pyrite in the Black Sea and the Sea of Azov. Similar deposits of iron sulfide, attributable to the activities of sulfate reducers, have been reported by Doss (1912) in the Mediterranean, Caspian, and Black Sea, by Ellis (1925) in the Clyde Sea Aestuary, by Kindle (1926) in the Bay of Fundy, by Strøm (1939) in Norwegian fjords, and by Copenhagen (1934) in Walvis Bay off the South African Coast. Manganese sulfide may be precipitated in a like manner. The formation of copper sulfide in marine sediments has been attributed to the activities of sulfate-reducing bacteria by Schneiderhöhn (1923), Trask (1925), Thiel (1926), and Bastin (1933). Thiel (1927) explained the formation of bauxite and other aluminum oxides from aluminous silicates as being partly due to the activities of sulfate-reducing bacteria.

Not only is sulfate in interstitial water reduced, but sulfate rocks in consolidated sediments may be attacked by sulfate-reducing bacteria. Gypsum, anhydrite, or other sulfate rocks may be slowly dissolved under conditions which are favorable for the activity of sulfate-reducing bacteria (ZoBell, 1947b). The dissolution of sulfate rocks is favored by low pH. The conversion of the strongly acidic sulfate radicle to neutral sulfur or to the only slightly acidic sulfide radicle tends to increase the pH, but the oxidation of organic compounds required as a source of energy for the sulfate-reducing bacteria generally yields acidic products, so the over-all effect may be to lower the pH. In one series of experiments, for example, Rittenberg (1941) found the final reaction of unbuffered media to be pH 5.8 to 5.9 as a result of the activity of sulfate reducers for 35 days in media having initial reactions of pH 6.0, 7.0, and 7.8, respectively.

The commonly reported occurrence of sulfate-reducing bacteria in the reservoir fluids in petroliferous marine sediments suggests that these bacteria may play a role in the formation or modification of petroleum. That such bacteria may modify the chemical composition of certain oil-field waters is quite generally accepted. The ability of some of them to attack petroleum hydrocarbons has been established (Tausson and Aleshina, 1932; Tausson and Vesselov, 1934; Novelli and ZoBell, 1944; Rosenfeld, 1947). The formation of liquid and waxy hydrocarbons by sulfate reducers has been reported by Jankowski and ZoBell (1944). Fatty acids ranging from acetic to stearic were also assimilated with the formation of small amounts of hydrocarbons in the cell substance of sulfate reducers.

Sulfate-reducing bacteria may have contributed greatly to the formation and migration of petroleum in ancient marine sediments by releasing oil from oil-bearing materials and promoting its flow. ZoBell (1947b) has shown that this may be done by dissolving either carbonate or sulfate rocks on which oil is adsorbed, by producing carbon dioxide which decreases the viscosity of oil, by the bacteria's displacing oil films physically, or by their producing detergents or surface active substances.

These bacteria are also of significance in the anaerobic corrosion of iron, a field actively investigated by Wight and Starkey (1945) and others.

It may also be mentioned that these organisms have been isolated from mineral waters of various spas and resorts in Europe and America (Gosling, 1904; Rank, 1907). One might speculate as to whether the sulfate reducers contribute to the "curative" properties of these waters or merely to their odors.

SUMMARY

Desulfovibrio aestuarii is described as the type species of marine bacteria which reduce sulfates as hydrogen acceptors in their energy-yielding reactions, although there may be other genera and species. Such bacteria are physiologically active only in the absence of free oxygen and they tend to maintain or create reducing conditions by producing hydrogen sulfide, particularly in stagnant water basins and in sedimentary deposits. Sulfate-reducing bacteria oxidize a large variety of organic compounds and some can utilize molecular hydrogen as an energy source.

Sulfate-reducers occur quite widely and abundantly in marine bottom deposits. They have also been found at appreciable depths in ancient marine sediments where they may play a part in petroleum formation. Besides affecting the pH, E_h, and organic content of bottom deposits, sulfate-reducers may be responsible for the formation of various metallic sulfides and the modification of other minerals in marine sediments.

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Contribution No. 389

AN ANALYSIS OF THE STIRRING AND MIXING PROCESSES IN INCOMPRESSIBLE FLUIDS

By

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INTRODUCTION

In the laboratory, the phenomena accompanying the mixture of two fluids are so commonplace that they do not seem to merit investigation. In the ocean and atmosphere, the phenomena are presumably very similar, but the lack of a good theory on which to base calculations complicates the problem much more than in the laboratory.

It is useful to consider a trivial experiment by way of introduction: the mixing of coffee and cream. Three more or less distinct stages can be observed:

1. *The initial stage,* in which rather large volumes of cream and coffee are distinctly visible; there are sharp gradients at the interfaces between the volumes, but elsewhere the gradient is practically zero. Averaged over the entire volume, the gradient is small. If motion of the liquids is avoided, this state persists for a considerable time.

2. *The intermediate stage,* after motion has been induced by stirring the liquids; the masses of cream and coffee are distorted, with a rapid increase in the extent of the interfacial regions having high concentration gradients. The average value of the gradient is correspondingly increased.

3. *The final stage,* in which the gradients disappear, apparently quite suddenly and spontaneously, with the liquid becoming homogeneous.

It is a reasonable working hypothesis to assume that these three stages (or at least the second and third) also occur in the ocean and atmosphere when concentration or temperature differences arise.

The potentially long duration of the first stage may be ascribed to the slowness of the diffusion or heat conduction process which results from the small average value of the gradients. During the second stage, the average value of the gradient is increased by the relative

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motion of different parts of the liquid as a result of stirring. The disappearance of the gradients during the third stage is presumably caused by molecular diffusion. This is more rapid than during the first stage, because stirring has increased the gradients and thus has also increased the diffusion currents. For convenience, this last stage may be called mixing, to distinguish it from stirring.

TWO EXAMPLES OF STIRRING

As a first example of stirring, one may consider the formation of a steep thermocline by lateral advection; Fig. 1 represents a vertical section of the fluid. Suppose that initially there is a small horizontal gradient, but that the regions *A* and *B* (Fig. 1a) are at appreciably different temperatures because of the relatively large distance separating them. Suppose further that the fluid everywhere moves horizontally, but that there is a vertical velocity gradient; the motion is laminar, with shear across the horizontal planes. Then, since the upper parts of the regions *A* and *B* move with a higher velocity than the lower parts, these regions will be distorted until eventually the configuration of Fig. 1b is produced. The particles 1 and 2 will have moved much closer together, although the temperature difference between them is unaltered. Thus the original small horizontal gradient will have been converted into a much larger vertical gradient.

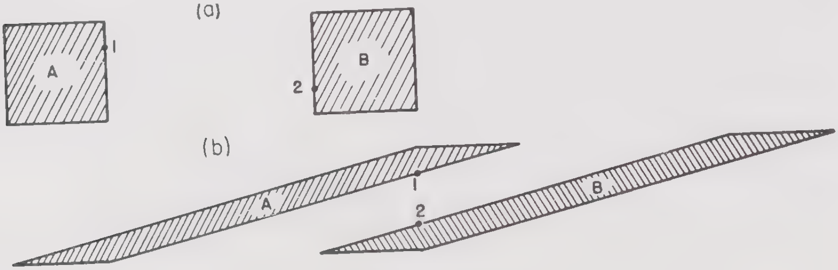

Figure 1. Stirring action of laminar flow.

This example suggests that the large thermal gradients shown on the bathythermogram of Fig. 2 may be indicative of regions of relatively large velocity gradients, and that the whole trace is indicative of horizontal shear in the layers between the depth of 120 and 240 feet. Possibly this suggestion could be tested experimentally.

As a second example, suppose the initial temperature distribution to be as before, but that an eddy is somehow set up with its axis horizontal and perpendicularly bisecting the line joining the centers of *A* and *B*

(Fig. 3a). In this eddy, let the orbits of the fluid particles be circular and be described with an angular velocity ω that is a function of their distance from the axis of the eddy. Then, after the lapse of successive intervals of time, the regions *A* and *B* of Fig. 3a will be deformed and assume the configuration shown in Figs. 3b and 3c. It is clear that such an eddying motion will be very effective, not merely in increasing the mean gradient but also in increasing the interfacial area of the regions *A* and *B* and in decreasing the interfacial distance between them. All three effects are such as to increase the flow of heat by conduction. During the stage of stirring these three processes dominate; ultimately they may so increase the conduction of heat that the latter dominates and causes the mean gradient to diminish toward zero.

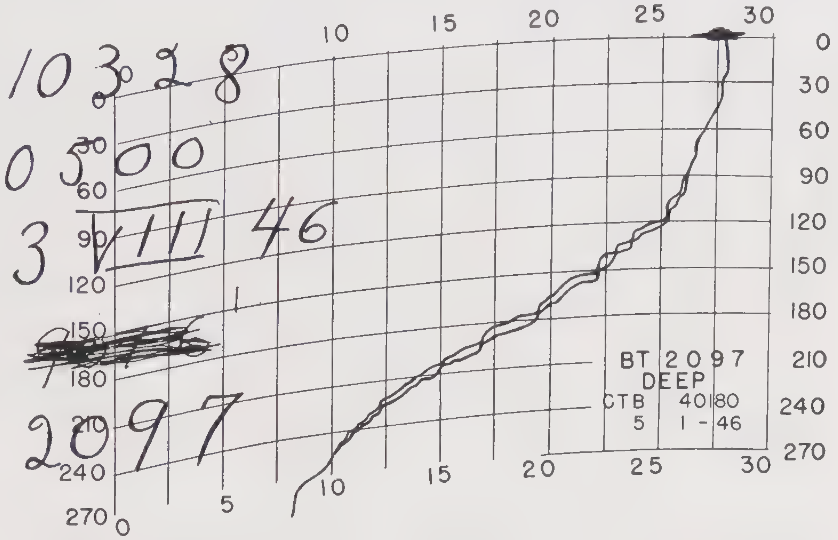

Figure 2. Bathythermogram taken on August 3, 1946, from U. S. S. INGRAHAM at Lat. 11° 48′ N., Long. 164° 46′ E. Temperature in °F., depth in feet.

It is not difficult to show that, because of the stirring action, the mean gradient at a distance *r* from the center of the eddy is

$$\tfrac{1}{2} \mid ar\,(d\omega/dr)\,t \mid,$$

where *a* is the initial horizontal gradient, and *t* is the elapsed time since the initial instant. Thus, if the eddy persists long enough, the gradient, and consequently the heat flow, may become very large indeed.

Having considered these two examples of stirring, the next section will examine the laws according to which heat conduction or diffusion operates to reduce the mean gradient. In the succeeding section, the manner in which these laws are modified by stirring will be treated in some generality.

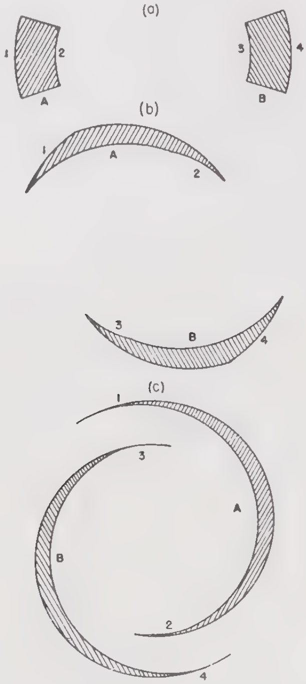

Figure 3. Stirring action of circular eddy.

THE EQUALIZATION OF GRADIENTS BY CONDUCTION OR DIFFUSION

In order to avoid, initially, the complication of the stirring process, consider conduction or diffusion in a solid substance. The differential equation governing this is

$$\frac{\partial \theta}{\partial t} = \kappa \, \nabla^2 \theta \,, \tag{1}$$

where κ is the conductivity or diffusion constant, and θ the temperature or concentration. On differentiating this, one obtains

$$\frac{\partial}{\partial t} \nabla \theta = \kappa \nabla^2 \nabla \theta \,; \tag{2}$$

multiplying scalarly by $\nabla\theta$, the result is

$$\begin{aligned}\frac{1}{2}\frac{\partial}{\partial t}(\nabla\theta)^2 &= \kappa\,\nabla\theta\cdot\{\nabla^2\,\nabla\theta\}\\ &= \kappa\,\nabla\cdot\{\nabla\theta\,\nabla^2\theta\} - \kappa\,\{\nabla^2\theta\}^2\\ &= \nabla\cdot\left\{\frac{\partial\theta}{\partial t}\nabla\theta\right\} - \kappa\left\{\nabla^2\theta\right\}^2. \end{aligned} \tag{3}$$

If one integrates the terms of this equation over a volume and uses the divergence theorem, the result is

$$\begin{aligned}&\frac{1}{2}\frac{d}{dt}\iiint\limits_{vol}(\nabla\theta)^2\,d\tau =\\ &\iint\limits_{bndry}\nu\cdot\nabla\theta\frac{\partial\theta}{\partial t}\,d\sigma - \kappa\iiint\limits_{vol}\{\nabla^2\theta\}^2\,d\tau,\end{aligned} \tag{4}$$

where $d\tau$ and $d\sigma$ are the elements of volume and area, and ν the unit vector normal to $d\sigma$.

At first, assume that the surface integral vanishes. This will certainly be the case if either: (a) the temperature of each point of the boundary is constant, so that $\partial\theta/\partial t = 0$, or (b) no heat flows through any point of the boundary, so that $\nu\cdot\nabla\theta = 0$. Then, since $\{\nabla^2\theta\}^2 \geqslant 0$, the right side of (4) is either negative or at most zero. Hence the integral on the left must decrease, or at most remain constant.

Define the rms gradient, G, by the equation

$$G^2 = \frac{1}{V}\iiint\limits_{vol}(\nabla\theta)^2\,d\tau, \tag{5}$$

where V is the volume of the region under consideration. The quantity I, defined by

$$I^2 = \frac{1}{V}\iiint\limits_{vol}(\nabla^2\theta)^2\,d\tau, \tag{6}$$

is a convenient measure of the inhomogeneity of the material inside V. Using these definitions,

$$\frac{1}{2}\frac{dG^2}{dt} = -\kappa I^2. \tag{7}$$

For a given inhomogeneity, therefore, the mean square gradient decreases at a rate *directly* proportional to the constant κ.

The activity of the material inside V is measured by the quantity A, defined by

$$A^2 = \frac{1}{V} \iiint\limits_{vol} \left(\frac{\partial \theta}{\partial t}\right)^2 d\tau \, . \tag{8}$$

Because of (1), (7) may also be written

$$\frac{1}{2} \frac{dG^2}{dt} = - \frac{1}{\kappa} A^2 \, . \tag{7.1}$$

For a given activity, the mean square gradient thus decreases at a rate *inversely* proportional to the constant κ.

However, the most important conclusion is that whenever the surface integral of (4) vanishes the rms value of the gradient never increases. In the case of a small solid object in the laboratory, the conditions for the surface integral to vanish are easily fulfilled. However, if an arbitrary volume of the ocean or the atmosphere is considered, this is no longer true. The conduction of heat through the boundary, and its consequent change in temperature, may become very important. Moreover, the process of stirring must be considered.

MODIFIED EQUALIZATION THEOREMS WHEN THE SUBSTANCE IS AN INCOMPRESSIBLE FLUID

When the substance under consideration is an incompressible fluid, rather than a solid, (1) becomes

$$\frac{D\theta}{Dt} = \kappa \nabla^2 \theta \, , \tag{10}$$

or, using the indicial notation,

$$\frac{D\theta}{Dt} = \kappa \frac{\partial^2 \theta}{\partial x_i^2} \, , \tag{11}$$

where

$$\frac{D}{Dt} = \frac{\partial}{\partial t} + u_i \frac{\partial}{\partial x_i} \, .$$

The differentiation of this equation (as above) encounters a complication, because

$$\frac{\partial}{\partial x_j} \frac{D}{Dt} = \frac{D}{Dt} \frac{\partial}{\partial x_j} + \frac{\partial u_i}{\partial x_j} \frac{\partial}{\partial x_i} \, . \tag{12}$$

The analogue of (2) is therefore

$$\frac{D}{Dt}\frac{\partial\theta}{\partial x_j} = \kappa\frac{\partial}{\partial x_j}\frac{\partial^2\theta}{\partial x_i^2} - \frac{\partial u_i}{\partial x_j}\frac{\partial\theta}{\partial x_i}, \tag{13}$$

and involves the velocity gradient $\partial u_i/\partial x_j$.

Multiplying by $\partial\theta/\partial x_j$, and summing,

$$\frac{1}{2}\frac{D}{Dt}\left(\frac{\partial\theta}{\partial x_i}\right)^2 = \kappa\frac{\partial}{\partial x_j}\left(\frac{\partial\theta}{\partial x_j}\frac{\partial^2\theta}{\partial x_i^2}\right) - \kappa\left\{\frac{\partial^2\theta}{\partial x_i^2}\right\}^2 - \frac{\partial u_i}{\partial x_j}\frac{\partial\theta}{\partial x_i}\frac{\partial\theta}{\partial x_j}. \tag{14}$$

In order to obtain simple integrated results, it is now necessary to choose a volume V whose boundary is not stationary but which moves so that it always encloses the same fluid. Integrating over such a moving volume, the result is

$$\frac{1}{2}\frac{dG^2}{dt} = \iint_{bndry} \nu \cdot \nabla\theta\frac{D\theta}{Dt}\,d\sigma - \kappa I^2 - S, \tag{15}$$

where the additional term is

$$S = \iiint_{vol} \frac{\partial u_i}{\partial x_j}\frac{\partial\theta}{\partial x_i}\frac{\partial\theta}{\partial x_j}\,d\tau \tag{16}$$

and is a measure of the rate at which stirring decreases the mean square gradient.

The other terms of (15) have been adequately discussed above, so that it remains only to discuss the integrand of (16). The velocity gradient is usually resolved into two components

$$\frac{\partial u_i}{\partial x_j} = u_{[ji]} + u_{(ji)}, \tag{17.1}$$

where

$$u_{[ji]} = \frac{1}{2}\left\{\frac{\partial u_i}{\partial x_j} - \frac{\partial u_j}{\partial x_i}\right\} \tag{17.2}$$

is recognized as being (except for a factor −½) the curl or vorticity of the motion, while the tensor

$$u_{[ji]} = \frac{1}{2}\left\{\frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i}\right\} \tag{17.3}$$

is called the deformation tensor and will be recognized from the familiar Stokes law of molecular viscosity.

It may be somewhat surprising to note that the integrand of (16) is independent of the curl, $u_{[ji]}$, but it can be shown that

$$\frac{\partial u_i}{\partial x_j}\frac{\partial \theta}{\partial x_i}\frac{\partial \theta}{\partial x_j} = u_{(11)}\left(\frac{\partial \theta}{\partial x_1}\right)^2 + 2u_{(12)}\frac{\partial \theta}{\partial x_1}\frac{\partial \theta}{\partial x_2} + 2u_{(13)}\frac{\partial \theta}{\partial x_1}\frac{\partial \theta}{\partial x_3} + u_{(22)}\left(\frac{\partial \theta}{\partial x_2}\right)^2 + 2u_{(23)}\frac{\partial \theta}{\partial x_2}\frac{\partial \theta}{\partial x_3} + u_{(33)}\left(\frac{\partial \theta}{\partial x_3}\right)^2.$$

This is an important result, because it is known that curl or vorticity is very difficult to generate in a large mass of fluid whose coefficient of viscosity is small. If it should have appeared that the opposite were true, that S depended only on the curl, then the hypothesis under investigation would have to be rejected. Such a result would have made the process of mixing so strongly dependent on viscosity as to be untenable. The astonishment at the result arises from the popular confusion of curl or vorticity with eddy motion. The second example above shows that eddy motion is very effective in mixing, possibly more so than laminar motion. On the other hand, it is a fact that in laminar motion the curl cannot be zero, whereas it is easy to give an example of eddy motion with circular orbits for which the curl vanishes; e. g., $\omega(r) = 1/r$. Thus, there is no inconsistency between (16) and the two examples discussed earlier.

In the examples, and in the more general discussion of stirring, it was indicated that the effect of the velocity gradients is usually to increase the mean temperature or concentration gradients. Therefore, it might be expected that the quantity S is always negative. This cannot be proven; in the case of an incompressible fluid, the velocity must satisfy the equation

$$\nabla \cdot u = 0,$$

or

$$u_{(11)} + u_{(22)} + u_{(33)} = 0\,.$$

Hence, usually at least one of the three terms of this equation (say $u_{(11)}$) will be positive and at least one (say $u_{(22)}$) will be negative. Under these conditions, a gradient having the x_1 direction would make $S > 0$, while a gradient having the x_2 direction would make $S < 0$. Thus S may have either sign, and stirring may sometimes have the effect of decreasing the mean gradient. This situation will be clarified by a re-examination of the first example.

MORE DETAILED EXAMINATION OF MIXING BY LAMINAR FLOW

The example of stirring by laminar motion is simple enough so that fairly detailed calculations can be made. If the temperature (or concentration) at time $t = 0$ is

$$\theta = ax + by + c\ , \tag{18}$$

it is required to find a solution of

$$\frac{\partial \theta}{\partial t} + u(y)\frac{\partial \theta}{\partial x} = \kappa\, \nabla^2 \theta\ , \tag{19}$$

which also reduces to (18) when t vanishes.

When $\kappa = 0$, this solution is unique, being

$$\theta \equiv \theta_o = a[x - u(y)t] + by + c\ . \tag{20}$$

This represents the effect of advection or stirring. The component of the gradient in the y-direction is

$$\frac{\partial \theta}{\partial y} = b - at\frac{du}{dy}\ .$$

For small values of t, its magnitude may either increase or decrease, depending on the relation between a, b and du/dy. For sufficiently large values of t, however, the second term must dominate, and hence the magnitude of the gradient will ultimately increase.

This illustrates two general propositions. It has already been noted above that advection may either increase or decrease the gradients. The new proposition is that, ultimately, advection usually increases the magnitude of the gradient. This is not without exception. In the textbook example of small surface waves, the motion is everywhere periodic and everywhere has the same period. Consequently, the changes caused by advection must also be periodic and they therefore constitute an exception to the rule. Actual surface waves, however, are not periodic, and their advective effects presumably conform to the rule. Because of these exceptional cases, a general proof of the proposition will be difficult and will be analogous to the proof of the ergodic theorem.[2]

Turning next to the case $\kappa \neq 0$, one may set

$$\theta = \theta_o + \vartheta\ , \tag{21}$$

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[2] G. D. Birkhoff. Proof of a recurrence theorem for strongly transitive systems Proc. nat. Acad. Sci., *17:* 650–655 (1931).

where ϑ is determined by the equation

$$\frac{\partial \vartheta}{\partial t} + u(y)\frac{\partial \vartheta}{\partial x} - \kappa\,\Delta^2\vartheta = -\,a\kappa t\frac{d^2u}{dy^2}\,. \tag{22}$$

At $t = 0$, one must require $\vartheta = 0$; it is characteristic that this requirement does not uniquely determine ϑ. Physically this means that conditions at the boundary of the medium are important: the sun may rise at some time after $t = 0$ and cause warming, etc.

However, special solutions of (22) can easily be obtained. One, which is independent of x, is the series

$$\vartheta = -\,a\sum_{m=2}^{\infty}\frac{\kappa^{m-1}t^m}{m!}\left(\frac{d}{dy}\right)^{2m-2}u(y)\,, \tag{23}$$

which can be considered as the solution that is applicable in the absence of such external effects as were just mentioned. It therefore determines the mixing process that is induced by laminar flow.

Since the series for ϑ begins with a term in t^2, it follows that, for sufficiently small values of t, the effect of mixing will be negligible compared to the advective effect which is measured by the term $-\,aut$ in (20). The time, t_c, at which the first term of the series for ϑ becomes equal to the advective term, is given by

$$t_c = 2u\bigg/\left(\kappa\frac{d^2u}{dy^2}\right)$$

and is a function of y.

Since $u/(d^2u/dy^2)$ has the dimensions of an area, it may be set equal to l^2, where l is a length that measures the homogeneity of the velocity distribution. Hence

$$t_c = 2l^2/\kappa. \tag{24}$$

For water, the thermal diffusion constant is $\kappa = 1.4 \times 10^{-3}$ cm^2/sec., while for the diffusion of dissolved salts, $\kappa = 2 \times 10^{-5}$ cm^2/sec. This leads to the following values for t_c:

MIXING TIMES

l	thermal	salt
1 m.	168 d.	32 yr.
1 cm.	24 min.	28 hr.
0.1 mm.	0.15 sec.	10 sec.

These values suggest that the saline microstructure of the sea may be much more pronounced than the thermal microstructure, since diffusion can scarcely counteract the effect of mixing.

The solution for ϑ in the case of a circular eddy is more complicated but should be derivable without excessive difficulty.

THE EFFECT OF VISCOSITY

The two examples considered above are both steady states of flow, and it is unlikely that steady motion will persist over the relatively long time interval t_c. In particular, it can be shown that viscosity will usually modify the motion considerably in such a length of time, unless it is balanced by a suitable pressure distribution.

The viscous effects are governed by equations that are very analogous to (10), except that κ is replaced by the kinematic viscosity n. For water n/κ (Prandtl's number) has the value 7.5. Consequently, the viscous effects will become appreciable in a time that is less than that required for thermal mixing. They will, in general, tend to increase l and hence slow down the mixing process. However, this tendency may be counteracted by pressure gradients or wind stresses.

CONCLUSIONS

1. In all except certain very special cases, advection alone will ultimately increase the mean value of any initial gradient.
2. This effect of advection is appropriately called stirring.
3. Stirring is independent of the vorticity of the motion and can occur even if the motion is not turbulent. It may be the explanation of the high gradients shown by some bathythermograms.
4. The effect of conduction or diffusion is to decrease the mean value of the gradient.
5. This is appropriately called mixing.
6. Ordinarily, the early stages of a process in which both stirring and mixing occur will be dominated by the advective processes.
7. These may so increase the mean gradient that the mixing process will ultimately dominate over the stirring process.
8. Viscosity, if not counteracted by other factors, tends to stop the stirring process before an appreciable amount of mixing can occur.

Contribution No. 390

Number 512 November 26, 1948

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

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HADROPTERUS NOTOGRAMMUS, A NEW PERCID FISH FROM MARYLAND, VIRGINIA, AND WEST VIRGINIA[1]

By Edward C. Raney and Carl L. Hubbs

In recent years only 1 species of the percid genus *Hadropterus,* namely the shielded darter, *Hadropterus peltatus,* has been recognized as an inhabitant of the Atlantic coastal drainage basins between the James and the Hudson river systems. Another darter of this area, originally named *Hadropterus sellaris* (Radcliffe and Welsh, 1913: 31–32, Pl. 18), has been referred by Hubbs and Black (1940: 3) to the genus *Poecilichthys.* This species, known only from 2 type specimens taken in Swan Creek near Havre de Grace, Maryland, shows none of the enlarged spiny scales along the mid-ventral line or between the pelvic fins, which, in part, characterize *Hadropterus.* Recent efforts to obtain more specimens by seining in Swan Creek have proved fruitless.

Studies of all available specimens of *Hadropterus* from the Atlantic drainage now prove that a second species, herein named *Hadropterus notogrammus,* is present in tributaries of Chesapeake Bay from the Patuxent River system of Maryland south to the James River system of Virginia and West Virginia

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[1] Contribution from the Department of Zoology, Cornell University, and from the Scripps Institution of Oceanography, New Series, No. 390.

(Map 1). It has been confused with *Hadropterus peltatus,* a very similar species that occurs in the same stream systems as well as in others farther north and farther south. At 3 places the species have been collected together. These 2 darters are closely related to the blackside darter, *Hadropterus maculatus* (Girard), a fish of widespread distribution west of the Appalachian Mountains.

The cotypes of *Hadropterus maculatus* (Girard, 1859*b:* 100), in the United States National Museum (No. 1157), upon re-examination prove to be the species herein described as new. The name, however, is preoccupied by that of the western species *Alvordius maculatus* Girard (1859*a:* 67–68), which, following Hubbs (1926: 59–60), has been identified with the species previously called *Hadropterus aspro* (Cope and Jordan). The label with the cotypes of *Hadropterus maculatus* and the catalogue entry bear the data, Patuxent, Maryland. This locality we regard as probably correct, even though Girard (1859*b:* 100) gave as the type locality "an eastern tributary of the Potomac River, in Anne Arundel, Md." The Patuxent River drains Anne Arundel County, and *Hadropterus notogrammus* is still common there. This darter has been recognized as a valid species by few subsequent ichthyologists (see synonymy).

The pertinent material has been studied with the kind permission and co-operation of the curators in charge of the several collections. The specimens in the University of Michigan Museum of Zoology (U.M.M.Z.) were made available by Reeve M. Bailey. Those in the United States National Museum (U.S.N.M.) were loaned by Leonard P. Schultz. In addition, numerous specimens were seined in the Potomac River system by Robert R. Miller. The example in the American Museum of Natural History (A.M.N.H.) was kindly sent by Charles M. Breder, Jr. Other material was obtained from the Museum of Comparative Zoology through the kindness of William C. Schroeder. When we visited the Academy of Natural Sciences of Philadelphia, Henry W. Fowler made certain specimens available for examination. We are particularly grateful to

Lincoln C. Pettit, now of the Biology Department, St. Lawrence University, who made a special effort to collect the holotype and a series of paratypes in the James River system, Virginia. Funds supplied by the Trustee-Faculty Committee on Research, Cornell University (C.U.), made possible the collection of many of the specimens taken by E. C. Raney and assistants.

STRIPEBACK DARTER

Hadropterus notogrammus, new species

(Pl. I, Figs. 1–2; Pl. II, Figs. 1–2; Map 1)

Hadropterus maculatus (preoccupied by *Alvordius maculatus* Girard, 1859*a:* 67–68, also a species of *Hadropterus*).—Girard, 1859*b:* 100 (original description; ''an eastern tributary of the Potomac River'' [properly a tributary of the Patuxent River], Anne Arundel County, Maryland). Putnam, 1863: 4 (*Alvordius maculatus* Girard, 1859*a:* 67, considered a synonym).

Etheostoma maculatum.—Cope. 1869*a:* 401 (characters). Cope, 1870*a:* 261–62 (characters; misidentification); 1870*b:* 449 (misidentification). Jordan and Copeland, 1876: 135, 164 (misidentification, in part; range, Pennsylvania to North Carolina, in part).

Alvordius maculatus.—Jordan, 1877: 14 (Pennsylvania to North Carolina); 1878: 220 (range and synonymy, in part). Pratt, 1935: 118 (range in part, including James River).

Etheostoma blennioides (misidentifications).—Cope, 1869*b:* 211 (confused; record, headwaters of the James). Jordan, 1876: 222 (range and synonymy, in part).

Alvordius aspro (misidentification).—Jordan, 1880: 220, and 1884: 220 (range and synonymy, in part).

Etheostoma aspro (misidentification).—Jordan, 1890: 112 (characters; James River at Lick Run).

Hadropterus aspro (misidentification).—Pratt, 1923: 125 (range in part, including James River).

Alvordius nevisensis (misidentification).—Jordan and Gilbert, 1883: 502 (Maryland).

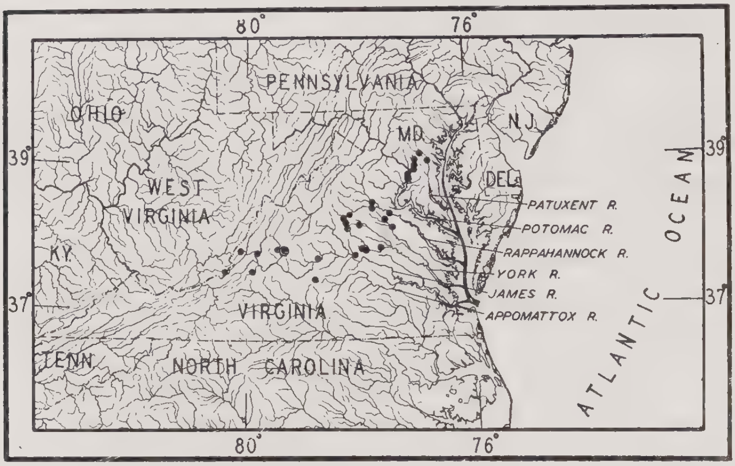
Etheostoma peltatum (misidentification).—Jordan, 1890: 113 (*H. maculatus* considered a synonym of *E. peltatum*).

Hadropterus peltatus (misidentifications).—Jordan, 1885: 867 (synonymy in footnote; confused). Jordan and Evermann, 1896:

1034 (considered a synonym of *H. maculatus*). Smith and Bean, 1899: 186 (Anne Arundel County, Maryland, and the upper Patuxent River). Radcliffe and Welsh, 1913: 32 (*H. peltatus* and *H. notogrammus* both used in preparation of table). Fowler, 1923: 10 (comparison). Truitt, Bean, and Fowler, 1929: 80–81 (Maryland records; two species confused).

Alvordius peltatus (misidentification).—Jordan, Evermann, and Clark, 1930: 283 (*H. maculatus* considered a synonym).

Hadropterus peltatus crassus (misidentification).—Fowler, 1945: 37, 136 (in synonymy; James River system?; species confused).


80°
76°
PENNSYLVANIA
OHIO
N.J.
MD
39°
39°
WEST VIRGINIA
DEL
PATUXENT R.
POTOMAC R.
RAPPAHANNOCK R.
YORK R.
JAMES R.
APPOMATTOX R.
OCEAN
KY
37°
37°
VIRGINIA
TENN
NORTH CAROLINA
ATLANTIC
80°
76°

MAP 1. Distribution of *Hadropterus notogrammus*, with all known record stations, all based on specimens examined. The type locality is ringed. Shown also are the river systems inhabited and the former downstream courses of these rivers as tributaries of the Pleistocene extension of the Susquehanna River, now dismembered by the late Quaternary rise in sea level. The stations were plotted by E. C. Raney and the map drafted by Norman J. Wilimovsky, on a part of the drainage map of the United States (July, 1940) that was prepared under the direction of Carl L. Hubbs, chiefly from the base map of the United States Geological Survey.

MATERIAL

Of this species, we have examined 7 type series and 31 nontype sets, listed below by stream systems. The collecting stations are indicated as dots on Map 1.

Upper James River System

The holotype, a male, 67 mm. in standard length, was collected by Lincoln C. Pettit on May 17, 1941, in South River, a tributary of North River, James River system, 5 miles east of Lexington, Rockbridge County, Lexington quadrangle, Virginia. U.M.M.Z., No. 144696. The dot for the type locality on Map 1 is ringed.

All paratypes are also from the upper, montane part of the James River system, and all are from Virginia, except for one lot from West Virginia. They bear the following data:

U.S.N.M., No. 40242: 1 female, 53.5 mm. long, obtained by D. S. Jordan on September 8, 1888, in James River at Lick Run, near the Alleghany–Botetourt county line, Virginia.

C.U., No. 8324: 4 adults, 47 to 58 mm. long, collected by E. C. Raney and E. A. Lachner on March 31, 1940, in Catawba Creek, 2 miles north of Fincastle, Botetourt County, Virginia.

C.U., No. 9708 and U.M.M.Z., No. 144697: 10 adults, 46 to 56 mm. long, collected by L. C. Pettit on May 17, 1941, in North River, Rockbridge County, Virginia.

C.U., No. 10138: 1 female, 55 mm. long, secured by Pettit on October 27, 1940, in North River, Rockbridge County, Virginia.

C.U., No. 4909: 2 adults, 53 and 54 mm. long, taken by A. H. Wright on July 28, 1931, in Potts Creek, Monroe County, West Virginia.

U.M.M.Z., No. 95194: 1 female, 42 mm. long, seined by Carl L. and Laura C. Hubbs on September 10, 1928, in Dunlap Creek at Callaghan, west of Covington, Alleghany County, Virginia.

Additional specimens, with data as follows, have been examined from other river systems. These are not designated as paratypes.

Middle James and Appomattox River Systems

U.S.N.M., No. 107497: 1 juvenile, 39 mm. long, collected by L. P. Schultz and E. D. Reid on October 11, 1938, in Byrd Creek east of Columbia, Goochland County, Virginia.

A.M.N.H., No. 8023: 1 male, 40 mm. long, collected by E. R. Dunn at Midway Mills, Nelson County, Virginia.

U.S.N.M., No. 100190: 2 males, 55 and 69 mm. long, taken by Stuart Abraham on April 22, 1935, in Appomattox River between Appomattox Court House and Vera, Appomattox County, Virginia.

York River System

C.U., No. 10528: 3 adults, 41 to 55 mm. long, collected by Raney, Lachner, and R. D. Ross on June 19, 1946, in Cub Creek, a tributary of South Anna River, 2.5 miles north of Gum Springs, Louisa County, Virginia.

U.S.N.M., No. 107746: 15 adults, 51 to 60 mm. long, collected by Schultz and Reid on September 29, 1938, in New Found River, a tributary of South Anna River, 3.5 miles above its mouth, Hanover County, Virginia.

U.S.N.M., No. 107715: 3 juvenile to adult specimens, 33 to 52 mm. long, taken by Schultz and Reid on September 29, 1938, in North Anna River, 8 miles north of Louisa, Louisa County, Virginia.

U.S.N.M., No. 107705: 1 juvenile, 36 mm. long, obtained by Schultz and Reid on September 28, 1938, in South Anna River, 3.5 miles south of Gordonsville, Louisa County, Virginia.

U.S.N.M., No. 100227: 1 female, 42 mm. long, collected by Abraham on April 24, 1935, in South Anna River at U. S. Highway 15 crossing south of Orange, Orange County, Virginia.

U.S.N.M., No. 119842: 3 adults, 39 to 53 mm. long, secured by M. C. Marsh on September 27, 1897, in Mattaponi River at Milford, Caroline County, Virginia.

U.S.N.M., No. 119850: 10 adults, 38 to 60 mm. long, taken by Schultz and Reid on September 29, 1938, in Cub Creek, 1 mile above mouth and 5 miles north of Gum Springs, Louisa County, Virginia.

U.M.M.Z., No. 102326: 14 adults, 46 to 60 mm. long, taken by Hubbs and group on May 6, 1934, in Ni River about 10 miles south of Fredericksburg on U. S. Highway 1, Spotsylvania County, Virginia.

Rappahannock River System

U.S.N.M., No. 107478: 8 juvenile to adult specimens, 36 to 59 mm. long, collected by Schultz and Reid on October 12, 1938, in Blue Run, 6 miles west of Orange, Orange County, Virginia.

U.S.N.M., No. 88651: 1 adult female, 38 mm. long, collected by Reid on October 7, 1927, at the mouth of Wilderness Run, Orange County, Virginia.

C.U., No. 10193: 4 adults, 41 to 64 mm. long, collected by Raney, Lachner, and R. A. Pfeiffer on March 28, 1941, in the Rappahannock River at Fredericksburg, Stafford County, Virginia.

C.U., No. 10527: 3 adults, 48 to 65 mm. long, collected by Raney, Lachner, and Ross on June 19, 1946, in Rapidan River at Madison Mills, Madison County, Virginia.

C.U., No. 10999: 3 adults, 50 to 60 mm. long, secured by Raney, Ross, and R. D. Suttkus on April 13, 1947, in a tributary of Rappahannock River, one-half mile east of Remington, Fauquier County, Virginia.

Potomac River System

U.S.N.M., No. 100643: 2 juveniles, 32 and 45 mm. long, taken by Abraham on May 30, 1935, in Middle Run, 15 miles south of Alexandria, Fairfax County, Virginia.

U.S.N.M., No. 100709: 1 male, 45 mm. long, collected by Abraham on May 27, 1935, in Cameron Run, one-half mile south of Alexandria, Fairfax County, Virginia.

U.S.N.M., No. 131784: 3 adults, 41 to 52 mm. long, seined by Robert R. Miller and C. C. Swears on August 27, 1944, in Point Branch, a tributary of Anacostia River, 1.5 miles above Old Powder Factory Road on the boundary of Montgomery and Prince Georges counties, Maryland.

U.S.N.M., No. 131798: 1 male, 58 mm. long, obtained by Miller and James Schultz on September 3, 1944, in Little Paint Branch, tributary to Anacostia River, between Beltsville and College Park, Prince Georges County, Maryland.

U.S.N.M., No. 74225: 7 adults, 41 to 68 mm. long, seined by Alfred C. Weed and Ernest B. Marshall on July 20, 1912, in Indian Creek at Beltsville, Prince Georges County, Maryland.

Patuxent River System

U.S.N.M., No. 106584: 2 females, 53 and 54 mm. long, taken by E. B. Marshall on April 18, 1937, in a tributary of Patuxent River at Laurel, Prince Georges County, Maryland.

U.S.N.M., No. 73322: 1 female, 53 mm. long, collected by E. B. Marshall on April 15, 1912, in Crow Branch near Laurel, Maryland.

U.S.N.M., No. 82612: 1 female, 59 mm. long, taken by George Marshall on July 15, 1918, in Fair Branch near Laurel, Maryland.

U.S.N.M., No. 74441: 1 male, 51 mm. long, collected by E. B. Marshall on June 14, 1912, at Laurel, Maryland.

U.S.N.M., No. 67433: 1 female, 52 mm. long, obtained by E. B. Marshall, in July, 1902, at Laurel, Maryland.

U.M.M.Z., No. 105519: 2 adults, 46 to 54 mm. long, taken by E. B. Marshall in 1938, in tributaries of Patuxent River, near Laurel, Maryland.

U.S.N.M., No. 1157: 2 males, 58 and 69 mm. long, secured by J. H. Clark at Patuxent, Maryland (cotypes of *Hadropterus maculatus* Girard, 1859*b*: 100).

U.S.N.M., No. 1303: 1 male, 58 mm. long, taken by S. F. Baird in a tributary of the Patuxent River in Anne Arundel County, Maryland.

U.M.M.Z., No. 144698: 2 specimens, 36 to 51 mm. long, collected by William H. Stickel on September 29, 1941, in Patuxent River at Telegraph Road, Patuxent Research Refuge, Anne Arundel County, Maryland.

U.M.M.Z., No. 138225: 1 female, 51 mm. long, secured by Ford Wilke and Robert E. Stewart on April 28, 1941, in Patuxent River at Patuxent Research Refuge, Prince Georges County, Maryland.

TABLE I

COMPARISON OF *Hadropterus notogrammus* WITH *Hadropterus peltatus*

Character	*H. notogrammus*	*H. peltatus*
Color markings along mid-line of back	Oval tan blotches (either disconnected or connected) are separated from the tan stripe along the upper side by a continuous pale streak.	Blackish saddles are interconnected, before and behind, by oblique extensions, so as to enclose oval light areas and to form a zigzag tan line along the upper back.
Dark nuchal blotch	Does not enclose a light oval area in the center and is separated from the origin of the dorsal fin by a light area.	Encloses near its center a light oval spot that, in turn, often has a small dark spot in its center; the blotch extends to the origin of the dorsal fin and there meets a light oval spot.
First dorsal fin	Rather uniformly dark (particularly in males) on the lower half of the membranes, especially on the anterior part of the fin.	Has a row of discrete black crescents, which form a conspicuous dark band just below the middle of the fin.
Dark caudal spot	Median	Lies below the middle of the tail base.
Dark blotches along sides	Mostly oval	Basically quadrate.
Lower side of head	Lacks the dark stripe behind the chin, although scattered melanophores may occur.	Has a dark stripe behind the chin.
Pigmentation on premaxillary	Dense on the sides, as well as in front.	Dense only on the front part.
Body	Slimmer, more pointed fore and aft when viewed from above, and more nearly oval in cross section.	Heavier, especially in the pectoral region; the head has a wider entering angle and is bluntish; the sides of the body are more nearly vertical.
Caudal fin	Has, when extended, a nearly straight posterior edge.	Emarginate.
Squamation on side of head	Cheek has some scales; opercle is completely scaled; subopercle is usually scaled.	Cheek is scaleless, or very nearly so; opercle is scaleless, or sparsely scaled dorsally; subopercle is scaleless.
Ventral scutes of males	Oval, armed with moderate spines.	Much longer than wide, armed with large spines.

RELATIONSHIPS

Although it has been confused for many years with *Hadropterus peltatus,* the only other species of the genus that is found within its range, *H. notogrammus* proves to be easily separable from that species. Table I as well as Plates I and II will facilitate their identification.

In addition to the more obvious distinctions enumerated in Table I, *H. notogrammus* differs from *H. peltatus* in many ways. The eye is longer than deep rather than about as long as deep. The eyes are more superolateral. The preorbital is narrower. The procurrent caudal rays are better developed. The ctenii on the scales are smaller. The mid-line of the belly in nearly all females is scaled just in front of anus, whereas in *peltatus* this region is scaleless. The general pigmentation of the body is more intense. The head is longer and less deep. The mouth is more oblique.

From *Hadropterus maculatus* (Girard), the species that is wide-ranging west of the Appalachian Mountains, *H. notogrammus* differs markedly in dorsal body pattern. In this respect *maculatus* is much like *peltatus* (Pls. I–II). The species *notogrammus* and *maculatus* are similar and they both differ from *peltatus* in the size and shape of the enlarged ventral scutes of the male, in the coloration of the spinous dorsal fin, in lacking a strong stripe of melanophores on the underside of the head behind the chin, and in the greater extension of melanophores onto the side of the premaxillary. Although in some parts of its range it is subject to considerable variation in these respects, *maculatus* contrasts with *notogrammus* in having finer scales, a longer and slenderer caudal peduncle, and the origin of the dorsal fin farther forward. From the robust *H. roanoka, notogrammus* is clearly differentiated on the basis of scale count (39 to 51, usually about 43 to 45, in *roanoka*) and by the distinctive coloration, as well as by the slenderer body. For a summary of the characters of other species of *Hadropterus,* none of which is closely related to *notogrammus,* see Bailey (1940 : 530).

TABLE II

COMPARISON BY RIVER SYSTEMS OF SCALE COUNTS OF
Hadropterus notogrammus

In the body of the table the figures in the first line for each rubric are the observed range and, in parentheses, the mean; those in the second line are the number of specimens and, in parentheses, the percentage separable above (+) or below (–) the arbitrary line of separation that is indicated in parentheses in the column heading. The frequency distributions are detailed in the Appendix.

River System	Number of Scales or Scale Rows				
	Lateral Line (60–61)	Above Lat. Line (7–8)	Below Lat. Line (9–10)	Around C. Ped. (21–22)	Along Midventral Line (8–9)
Patuxent	54–61 (57.2) 13 (92;–)	6–8 (6.9) 14 (93;–)	8–10 (9.1) 14 (71;–)	20–21 (20.9) 14 (100;–)	7–10 (8.5) 4 (50;±)
Potomac	51–59 (54.8) 15 (100;–)	6–8 (7.2) 15 (67;–)	9–11 (9.7) 15 (60;+)	20–23 (21.1) 15 (67;–)	9–11 (10.1) 8 (100;+)
Rappahannock	55–62 (58.8) 16 (75;–)	6–8 (6.9) 16 (87;–)	9–12 (9.8) 16 (63;+)	20–23 (21.2) 16 (75;–)	7–10 (8.4) 8 (63;+)
York	50–60 (54.5) 50 (100;–)	6–8 (6.7) 47 (94;–)	8–11 (9.2) 47 (72;–)	18–23 (20.5) 46 (85;–)	5–13 (7.8) 31 (68;–)
Upper James	57–65 (61.5) 20 (75;+)	6–8 (7.7) 20 (70;+)	8–11 (9.9) 20 (55;+)	20–24 (22.1) 20 (75;+)	8–13 (8.4) 13 (62;+)
Middle James and Appomattox	56–60 (58.3) 4 (100;–)	6–8 (7.0) 4 (75;–)	8–11 (9.7) 4 (75;+)	21–22 (21.7) 4 (75;+)	....
Total	50–65 (56.8) 118	6–8 (7.0) 116	8–12 (9.5) 116	18–24 (21.0) 115	5–13 (8.6) 64

DIAGNOSIS

Hadropterus notogrammus differs strikingly from its near relatives, *H. maculatus* and *H. peltatus,* in the color pattern of the back (Pl. II). A conspicuous pale streak on the dorsolateral body surface continues forward to set off the longitudinal dark nuchal blotch (or blotches). A pale cross band usually surrounds the front of the dorsal fin. Irregular oval dark blotches on the mid-line of the back sometimes touch each other but only rarely reach laterally to contact the continuous pale streak. Most of the 6 to 8 dark oval blotches along the side of the body are connected by a narrow median lateral stripe. Between the pale stripe and the dark lateral blotches lies a continuous zigzag tan stripe, which is edged below by a pale streak where it is not in direct contact with one of the black blotches. Black pigment on the spinous dorsal of a highly colored male is most pronounced on the lower half of the first 4 to 6 interradial membranes, but is also evident on the other membranes. This pigment becomes most intense near the base of the membranes, but does not form definite black crescents as it does in *Hadropterus peltatus.* The subocular and preocular dark bars are well developed. The scales, of moderate size, number 50 to 65 along the lateral line, 6 to 8 above the lateral line, 8 to 12 below the lateral line, and 18 to 24 around the caudal peduncle (Table II). From 5 to 13, usually 7 to 10, enlarged scales (Table II), each with spines of moderate length, lie along the mid-line of the belly of males (females lack these large scutes, but have a few small scales along the mid-line posteriorly). The cheek is partly scaled, usually bearing only a few small, more or less embedded scales on the upper third. The opercle is covered with scales of normal size. There is usually one row of scales on the subopercle, occasionally 2 rows. The nape is either naked or partly scaled; usually it bears only a scattering of small embedded scales; when normal scales are included they usually lie close to the origin of the dorsal fin. Dorsal rays, XII to XVI—11 to 14 (total, 23 to 29); anal rays, II, 8 to 10;

TABLE III

COMPARISON BY RIVER SYSTEMS OF FIN-RAY COUNTS AND MERISTIC INDEX OF *Hadropterus notogrammus*

For explanation see sublegend of Table II.

River System	Number of Rays and Meristic Index					
	Dorsal Spines (14–15)	D Soft Rays (11–12)	Total D Rays (26–27)	Anal Soft Rays (8–9)	Pectoral Rays (13–14) *	Meristic Index (67–68) †
Patuxent	12–14 (13.4) 14 (100;–)	11–13 (12.0) 14 (79;+)	24–27 (25.4) 14 (86;–)	8–10 (9.0) 14 (86;+)	13–14 (13.8) 28 (82;+)	59–67 (64.1) 14 (100;–)
Potomac	12–15 (13.1) 15 (93;–)	11–13 (11.8) 15 (73;+)	24–26 (24.9) 15 (100;–)	8–10 (8.9) 15 (80;+)	13–15 (13.9) 32 (81;+)	58–66 (61.6) 15 (100;–)
Rappahannock	13–15 (13.9) 16 (93;–)	11–13 (12.0) 16 (87;+)	24–27 (25.9) 16 (81;–)	8–10 (9.1) 16 (81;+)	13–15 (13.9) 32 (75;+)	61–71 (66.1) 16 (75;–)
York	12–15 (13.5) 47 (96;–)	11–13 (11.6) 47 (57;+)	23–27 (25.1) 47 (96;–)	8–10 (8.7) 47 (66;+)	13–15 (14.2) 92 (99;+)	55–65 (60.0) 44 (100;–)
Upper James	14–16 (14.7) 20 (65;+)	11–14 (12.3) 20 (80;+)	25–29 (27.1) 20 (65;+)	9–10 (9.4) 20 (100;+)	13–15 (13.8) 42 (69;+)	66–74 (70.1) 20 (90;+)
Middle James and Appomattox	14–15 (14.7) 4 (75;+)	11–12 (11.7) 4 (75;+)	26–27 (26.5) 4 (50;±)	9–9 (9.0) 4 (100;+)	13–15 (13.9) 8 (75;+)	64–68 (66.0) 4 (75;–)
Total	12–16 (13.7) 116	11–14 (11.9) 116	23–29 (25.6) 116	8–10 (8.9) 116	13–15 (14.0) 234	55–74 (63.6) 113

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* Each side tabulated.

† Computed for each specimen by subtracting the total number of pectoral rays from the sum of the lateral line scales, the dorsal spines and soft rays, and the anal soft rays.

pectoral rays, 13 to 15. The edge of the preopercle is smooth. The gill membranes are separate. The distance from the insertion of the pelvic fin to the union of the gill membranes goes 0.5 to 0.8 times into the distance from the tip of the mandible to the union of the gill membranes. Branchiostegal rays, 6. The head is relatively broad and the snout is rather short. The air bladder is present but small.

FURTHER DESCRIPTION

Many of the additional characters, such as those of body form and color pattern, are illustrated in Figures 1 and 2 on each of the plates. The scale counts are detailed by drainage system in Table II and the fin-ray counts in Table III. Counts for the holotype are: scales, 7—65—11 (the lateral line count is extreme for the species); scale rows around caudal peduncle, 22; dorsal rays, XV—12; anal rays, II, 9; pectoral rays, 13—13. The spinous and soft dorsal fins are slightly to moderately separated. Following the format employed by Hubbs and Raney (1939: 5–6) various body and fin measurements, including those for the holotype, are expressed as proportions in Table IV. Counts and measurements were made in accordance with the recommendations by Hubbs and Lagler (1941: 12–20; 1947: 8–15). Other descriptive items, based on the holotype and paratypes (from the upper parts of the James River system), follow.

HEAD CHARACTERS

The vertical arm of the preopercle is slightly longer than the horizontal arm. The width of the premaxillary frenum equals the distance between the anterior and posterior nostrils, enters the length of the eye 2.5 times, and is slightly greater than the width of the fleshy anterior tip of the upper lip. In the holotype the width of the mandibular frenum goes 1.5 times into the width of the premaxillary frenum and the lower jaw is included within the somewhat bluntly rounded snout. Some small paratypes, in contrast, have the snout sharper. In lateral view, the lower edge of the upper lip

TABLE IV

Measurements of 34 Specimens of *Hadropterus notogrammus*

The measurements were taken with dividers and stepped into the part indicated. Averages are in parentheses.

River system	Patuxent	Potomac	Rappahannock	York	Upper James		Total Range and Average
No. of specimens	6	6	6	6	9 Paratypes	Holotype	34
Standard length, mm.	52–58 (53.5)	44–66 (53.8)	48–63 (56.7)	53–57 (55.3)	44–56 (51.6)	67	44–66 (53.8)
In standard length:							
Depth of body	4.7–5.4 (5.1)	5.1–5.5 (5.3)	4.8–5.1 (5.0)	4.7–5.0 (4.9)	4.7–5.6 (5.2)	5.5	4.7–5.6 (5.1)
Length of head, including opercular membrane	3.2–3.5 (3.4)	3.3–3.5 (3.4)	3.3–3.4 (3.4)	3.2–3.4 (3.3)	3.3–3.6 (3.4)	3.4	3.2–3.6 (3.4)
In length of head:							
Depth of caudal peduncle	2.9–3.2 (3.0)	3.0–3.1 (3.0)	2.9–3.0 (3.0)	2.9–3.1 (3.0)	2.9–3.0 (3.0)	3.1	2.9–3.2 (3.0)
Highest dorsal spine	2.2–2.7 (2.5)	2.2–2.8 (2.5)	2.1–2.9 (2.4)	2.3–2.6 (2.4)	2.2–2.8 (2.5)	2.6	2.1–2.9 (2.5)
Highest dorsal soft ray	1.9–2.1 (2.0)	2.0–2.2 (2.1)	1.9–2.0 (2.0)	1.9–2.0 (2.0)	1.9–2.3 (2.1)	2.1	1.9–2.3 (2.0)
Highest anal ray	1.9–2.0 (1.9)	1.8–1.9 (1.9)	1.7–2.1 (1.9)	1.7–2.0 (1.9)	1.8–2.1 (1.9)	2.0	1.7–2.1 (1.9)
Longest caudal ray	1.3–1.6 (1.4)	1.3–1.4 (1.4)	1.3–1.5 (1.4)	1.3–1.5 (1.4)	1.2–1.7 (1.4)	1.7	1.2–1.7 (1.4)

TABLE IV—(*Cont.*)

River system	Patuxent	Potomac	Rappahannock	York	Upper James		Total Range and Average
					Paratypes	Holotype	
Length of pectoral fin	1.2 (1.2)	1.1–1.2 (1.1)	1.1–1.2 (1.1)	1.1–1.2 (1.1)	1.0–1.1 (1.1)	1.1	1.0–1.2 (1.1)
Length of pelvic fin	1.3–1.4 (1.3)	1.3–1.4 (1.3)	1.3–1.5 (1.4)	1.3–1.4 (1.4)	1.2–1.5 (1.4)	1.4	1.2–1.5 (1.4)
Depth of head	1.7–1.9 (1.8)	1.8–1.9 (1.8)	1.7–1.8 (1.8)	1.8–1.9 (1.9)	1.8–2.0 (1.8)	1.8	1.7–2.0 (1.8)
Width of head	1.8–2.0 (1.9)	1.7–1.9 (1.9)	1.7–1.9 (1.8)	1.8–2.0 (1.9)	1.7–2.0 (1.9)	1.7	1.7–2.0 (1.9)
Length of eye	3.7–4.2 (4.1)	3.8–4.3 (4.1)	3.9–4.4 (4.1)	4.1–4.5 (4.2)	3.7–4.1 (4.0)	4.3	3.7–4.5 (4.1)
Length of snout	3.8–4.1 (3.9)	3.9–4.2 (4.0)	4.0–4.1 (4.0)	4.0–4.4 (4.2)	3.9–4.2 (4.0)	4.3	3.8–4.4 (4.0)
Length of upper jaw	3.4–3.6 (3.5)	3.1–3.4 (3.2)	3.1–3.3 (3.1)	3.1–3.5 (3.3)	3.1–3.3 (3.2)	3.1	3.1–3.6 (3.3)
In length of snout:							
Length of eye	0.9–1.0 (1.0)	0.9–1.1 (1.0)	0.9–1.1 (1.0)	0.9–1.1 (1.0)	0.9–1.0 (1.0)	1.0	0.9–1.1 (1.0)

TABLE IV—(*Cont.*)

River system	Patuxent	Potomac	Rappahannock	York	Upper James		Total Range and Average
					Paratypes	Holotype	
In length of eye:							
Least fleshy interorbital width	1.3–1.7 (1.5)	1.5–1.8 (1.6)	1.5–1.8 (1.6)	1.2–1.6 (1.4)	1.5–1.8 (1.6)	1.9	1.2–1.9 (1.6)
Least bony interorbital width	2.0–2.3 (2.1)	2.0–2.4 (2.2)	2.1–2.4 (2.2)	2.0–2.1 (2.1)	2.0–2.2 (2.1)	2.3	2.0–2.4 (2.1)
In distance from tip of mandible to union of gill membranes:							
Distance from insertion of pelvic fin to union of gill membranes	0.6–0.8 (0.7)	0.6–0.8 (0.7)	0.6–0.8 (0.7)	0.6–0.7 (0.6)	0.6–0.8 (0.7)	0.5	0.5–0.8 (0.7)

is curved gently downward near the anterior tip. The upper lip rises almost to the level of the center of the eye. The mandibles are gently curved. The vomer bears a small triangular patch of teeth; each palatine, an interior row of rather small depressible teeth and an outer row of minute teeth. In the jaws rather strong teeth are aligned in the outer row and smaller interior teeth form a narrow, scarcely more than biserial, band. The gill rakers number 2 + 13 in the holotype. The 2 on the upper arm and the uppermost 9 on the lower arm are large. The longest, the first on the lower arm, when depressed extends only slightly beyond the base of the first raker below.

LATERAL LINE STRUCTURES

The lateral canal of the head, as is usual in darters, has 5 pores. The anterior nasal pore opens in front of and above the anterior nostril, and it connects with the canal by a short posteriorly extending tube. The posterior nasal pore opens just above the posterior nostril and enters the canal by a slender tube that extends mesad and forward from the pore. The interorbital pore opens at a point above the front border of the pupil and connects with the canal by a tube that extends forward and mesad. The single coronal pore is located at the end of a slender, slightly curved tube which extends backward from the canal. The postorbital pore opens immediately anterior to the canal and joins it by a short tube. The 8-pored infraorbital canal is complete. The operculomandibular canal has 10 pores. The median pore of the complete supratemporal commissure is at the end of a backward extending canal. (See Hubbs and Cannon, 1935, Pl. 2, for explanation of terms.) The lateral line is straight and complete.

GENITAL PAPILLA

The genital papilla of the male, located just posterior to the anus, is a flattened fleshy flap that is rounded behind and extends backward almost to the base of the first anal ray.

The posterior edge is slightly notched in the center in some males, and in the holotype there is an extra flap on the left side that presumably is a regenerated piece, since the papilla appears to have been injured. In the female the papilla is a larger semirectangular flap that is somewhat fimbriate on the posterior border, where the longitudinal creases and folds on the ventral side of the flap converge.

SPECIALIZED VENTRAL SCALES

Each of the 5 to 13 enlarged scales along the mid-line of the belly of the adult males is almost circular, with a rather straight anterior border. There is some variation in the length of the spines, but the largest are about one-fifth the largest diameter of the scute. These spines usually vary from 3 to 6 and are deflected backward and downward. Occasionally, 1 of the enlarged median scales is flanked by a smaller, somewhat specialized scale.

Anteriorly the belly is naked in both sexes. As is usual in the genus, there is an enlarged scale just back of the pelvic fin base and another near the middle of the breast. Most females have small scales on the posterior one-third to one-half of the belly. Although normally these scales are not specialized, some are slightly enlarged and have small spines on the posterior border.

In the holotype, five embedded scales lie immediately behind the enlarged breast scale. Just anterior to the anus, on either side of the mid-line, in this specimen and in some others, are two scutes of moderate size. The large scales on the mid-line of the holotype number 11. Most paratypes also have some small scales on the breast, but some specimens are naked in this area.

COLORATION

The life colors of a female taken by Carl L. and Laura C. Hubbs on September 10, 1928, in Dunlap Creek, at Callaghan, Alleghany County, Virginia, follow: the dark lateral oval blotches are blue-black; the light areas of the cheeks, the light bars on the spinous dorsal fin, the dorsolateral stripe of the body, and the areas around the dark lateral blotches are golden; other light areas on the sides and back and between the mandibles are amber; the mandibles are bright metallic blue.

In alcohol the oval blotches (usually 7) are black and the darker areas on the back are tan. The dark blotches along the mid-side contrast with the light lower sides and belly. The dark spot at the base of the caudal fin is median and on a level with the dark lateral stripe that connects the lateral blotches (in *H. peltatus* the spot lies below the lateral stripe). In some specimens this caudal spot is expanded vertically to form a bar. The ventral surface of the body is light, with an even scattering of melanophores, which are most conspicuous anteriorly and become most pronounced in the breeding males. Along the mid-line of the back, under the dorsal fin, are 7 small oval tan blotches, which may or may not be connected. Just laterad is a more or less uninterrupted light line that continues forward on either side of the semiquadrate nuchal blotch (or blotches), around the front of which it usually crosses the body to meet its fellow of the opposite side. Another light streak crosses the back just in front of the dorsal fin. Between the conspicuous light stripe and the lateral dark blotches is a tan stripe with irregular edges. It starts above the opercle and continues somewhat irregularly backward to below the second dorsal fin, where it tends to break up into oval blotches. Ventrally it sometimes fuses with the dark lateral blotches just below it on the side of the body, but seldom extends dorsally to touch the tan blotches on the dorsal mid-line.

On the top of the head are 2 light lines that run laterally backward behind the eye and connect with another somewhat fainter light line that lies just above the opercle. The top of the snout is rather evenly and heavily pigmented in breeding males and is spotted with tan in other specimens. A dark stripe begins on the snout, crosses the eye, and continues backward across the dorsal part of the cheek and then across the opercle, on which it is somewhat expanded ventrally. Its posterior extension on the body is more or less continuous with the dark lateral stripe. A dark subocular bar reaches ventrally to the lower limit of the cheek. In the breeding male there is much black in the membranes of the spinous dorsal fin. This black color is nearly solid on the ventral part of the first 5 or 6 interradial membranes; posteriorly, it is more limited to the center of the basal part of each membrane and is less intense; on the last few membranes, the intensity is slightly regained. On the soft dorsal, also, the dark pigment is concentrated on the interradial membranes, so as to give this fin a weakly banded appearance. The caudal has 3 or 4 rather faint vertical dark bands. In addition, the first few principal ventral and dorsal rays of the caudal are dusky near the base. The anal and pelvic fins are usually covered with small melanophores. The pectorals are somewhat less dusky. In nonbreeding males and in females the black is less intense on the fins, all of which tend to be somewhat barred.

INTRASPECIFIC VARIATION

Although its range (Map 1) is limited to the streams that flow from the west into the southern half of Chesapeake Bay and although these streams were undoubtedly tributaries of a great river that flowed through the shallow depression of this bay during the late Pleistocene lowering of sea level (Veatch and Smith, 1939: 44; Atwood, 1940: 36), *Hadropterus notogrammus* is by no means uniform in its characters. The samples from the several river systems differ rather markedly in certain meristic features (Tables II–III and Appendix). Some of the differences may be attributed to the isolation of populations since the connecting river was drowned by the formation of Chesapeake Bay, as a result of the rising sea levels that accompanied the recession of the Wisconsin icecap. *H. notogrammus* is a riffle species that avoids the base-level parts of the streams as well as the brackish waters of the arms of Chesapeake Bay.

The most marked variation, however, appears to have an ecological basis, which may have antedated the Wisconsin epoch of glaciation. The populations of the upper part of the Coastal Plain and of the Piedmont have on the average fewer scales and fewer fin rays than do those inhabiting the mountains. By far the highest counts characterize the samples from the upper part of the James River system—the only series that represent real montane habitats (compare Map 1 with Plate II in Fenneman's monograph, 1938). The next highest averages are exhibited by the series from the Rappahannock drainage system, which in the mountains abuts the James River system. Most of the Rappahannock samples, however, are from Piedmont streams. The specimens from the York system—from both the Mattaponi and the Pamunkey branches—have the lowest averages, and this system is cut off from the higher mountains by the branches of the Rappahannock and the James rivers. Farther north, perhaps because of a preference for relatively warm waters, this species seems to have been confined to the lowlands and for this reason did not follow *H. peltatus* in the Postglacial reinvasion of the Susquehanna, Delaware, and Hudson watersheds. In the Potomac system it seems to be confined to streams close to the head of tidewater, below the falls. The Patuxent is not a mountain stream. In correlation with the relatively low elevations, the counts are rather low for the most northern systems. The 4 fish from the middle part of the James system and from the short Appomattox River, which enters the James River near the head of its estuary, agree better with the specimens from the other systems than with those from the upper James (Tables II–III).

It is probable that the population of the upper montane part of the James River system will prove subspecifically distinct because of the higher counts. On the basis of the available data, differentiation on the subspecific level is definitely indicated. Using a meristic index, computed to maximize approximately the differences in the counts, it is possible to set a line (between indices 67 and 68) that will allow the separation of 90 per cent of the upper James specimens from 75 to 100 per cent of the specimens of other stocks (last column, Table III). By using the lateral line scale counts, with the division set between 60 and 61, it is possible to separate 75 per cent of the upper James fish from 75 to 100 per cent of those from other waters. Separability approaching that expected for subspecies is obtained for the counts of scales above the lateral line, of scale rows around the caudal peduncle, of the dorsal spines, and of total dorsal rays (though for the 3 latter tallies the 4 fish from the middle James and the Appomattox happen to agree best with those from the upper James).

Because of the limited amount of material available from the James it is deemed inexpedient at the moment to separate *Hadropterus notogrammus* into 2 subspecies. Should the study of further collections confirm the consistency of the high counts now shown only by material from the upper montane parts of the James River system, a new subspecies should be recognized for the populations that inhabit the other waters.

HABITAT

Small and medium streams appear to provide the optimum habitat for *Hadropterus notogrammus.* Small brooks are avoided except during the spring spawning migration. On one occasion *H. notogrammus* was taken in a river, the Rappahannock at Fredericksburg, Virginia, along with *H. peltatus.* Here both species were found among the boulders in the riffles below the falls under the U. S. Highway 1 bridge. During spring both species occur in moderate-sized streams, in and near riffles. At this time of year scuffing stones and kicking out weedbeds seem to be the most productive methods of collecting these darters. In the summer they are more common in the pools near riffles. They avoid strictly sand-bottomed streams.

The name *notogrammus,* derived from νωτος, ''back'' and γραμμή, ''a line,'' refers to the prominent light color streak along the back.

APPENDIX

SCALE AND FIN-RAY COUNTS OF HADROPTERUS NOTOGRAMMUS BY RIVER SYSTEMS

The number of specimens for each count is recorded in parentheses. The data are analyzed in Tables II and III.

LATERAL LINE SCALES.—*Patuxent:* 54(1), 55(2), 56(3), 58(4), 59(1), 60(1), 61(1). *Potomac:* 51(1), 52(3), 53(2), 54(3), 56(2), 58(1), 59(3). *Rappahannock:* 55(1), 57(4), 58(3), 59(2), 60(2), 61(2), 62(2). *York:* 50(2), 51(6), 52(3), 53(4), 54(10), 55(8), 56(6), 57(5), 58(3), 59(2), 60(1). *Upper James:* 57(1), 59(1), 60(2), 61(7), 62(5), 63(1), 64(1), 65(2). *Middle James and Appomattox:* 56(1), 57(1), 60(2).

SCALES ABOVE LATERAL LINE.—*Patuxent:* 6(2), 7(11), 8(1). *Potomac:* 6(2), 7(8), 8(5). *Rappahannock:* 6(4), 7(10), 8(2). *York:* 6(19), 7(25), 8(3). *Upper James:* 6(1), 7(5), 8(14). *Middle James and Appomattox:* 6(1), 7(2), 8(1).

SCALES BELOW LATERAL LINE.—*Patuxent:* 8(2), 9(8), 10(4). *Potomac:* 9(6), 10(8), 11(1). *Rappahannock:* 9(6), 10(8), 11(1), 12(1). *York:* 8(9), 9(25), 10(9), 11(4). *Upper James:* 8(1), 9(8), 10(4), 11(7). *Middle James and Appomattox:* 8(1), 10(2), 11(1).

SCALE ROWS AROUND CAUDAL PEDUNCLE.—*Patuxent:* 20(2), 21(12). *Potomac:* 20(6), 21(4), 22(3), 23(2). *Rappahannock:* 20(4), 21(8), 22(1), 23(3). *York:* 18(1), 19(4), 20(18), 21(16), 22(6), 23(1). *Upper James:* 20(1), 21(4), 22(9), 23(5), 24(1). *Middle James and Appomattox:* 21(1), 22(3).

ENLARGED SCALES ON MID-LINE OF BELLY OF MALE.—*Patuxent:* 7(1), 8(1), 9(1), 10(1). *Potomac:* 9(3), 10(1), 11(4). *Rappahannock:* 7(1), 8(2), 9(3), 10(2). *York:* 5(3), 6(3), 7(11), 8(4), 9(4), 10(4), 12(1), 13(1). *Upper James:* 8(5), 9(4), 10(1), 11(1), 12(1), 13(1).

DORSAL SPINES.—*Patuxent:* 12(1), 13(6), 14(7). *Potomac:* 12(5), 13(5), 14(4), 15(1). *Rappahannock:* 13(3), 14(12), 15(1). *York:* 12(4), 13(18), 14(23), 15(2). *Upper James:* 14(7), 15(11), 16(2). *Middle James and Appomattox:* 14(1), 15(3).

DORSAL SOFT RAYS.—*Patuxent:* 11(3), 12(8), 13(3). *Potomac:* 11(4), 12(10), 13(1). *Rappahannock:* 11(2), 12(12), 13(2). *York:* 11(20), 12(24), 13(3). *Upper James:* 11(4), 12(8), 13(7), 14(1). *Middle James and Appomattox:* 11(1), 12(3).

TOTAL DORSAL RAYS.—*Patuxent:* 24(2), 25(6), 26(4), 27(2). *Potomac:* 24(5), 25(7), 28(3). *Rappahannock:* 24(1), 25(3), 26(9), 27(3). *York:* 23(2), 24(7), 25(23), 26(13), 27(2). *Upper James:* 25(1), 26(6), 27(8), 28(3), 29(2). *Middle James and Appomattox:* 26(2), 27(2).

ANAL SOFT RAYS.—*Patuxent:* 8(2), 9(10), 10(2). *Potomac:* 8(3), 9(10), 10(2). *Rappahannock:* 8(3), 9(9), 10(4). *York:* 8(16), 9(30), 10(1). *Upper James:* 9(16), 10(4). *Middle James and Appomattox:* 9(4).

Pectoral rays (each side tabulated).—*Patuxent:* 13(5), 14(23). *Potomac:* 13(6), 14(24), 15(2). *Rappahannock:* 13(8), 14(20), 15(4). *York:* 13(1), 14(70), 15(21). *Upper James:* 13(13), 14(26), 15(3). *Middle James and Appomattox:* 13(2), 14(5), 15(1).

Meristic index (computed for each specimen by subtracting the total number of pectoral rays from the sum of the lateral line scales, the dorsal spines and soft rays, and the anal soft rays).—*Patuxent:* 59(1), 61(1), 62(1), 63(2), 64(1), 65(4), 66(2), 67(2). *Potomac:* 58(3), 59(3), 60(2), 62(1), 65(5), 66(1). *Rappahannock:* 61(1), 62(1), 63(1), 64(2), 65(1), 66(2), 67(4), 68(1), 69(1), 70(1), 71(1). *York:* 55(1), 56(6), 58(8), 59(2), 60(10), 61(4), 62(3), 63(5), 64(3), 65(2). *Upper James:* 66(2), 68(3), 69(3), 70(2), 71(4), 72(3), 73(2), 74(1). *Middle James and Appomattox:* 64(1), 66(2), 68(1).

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PLATE I

FIG. 1. *Hadropterus notogrammus:* side view of a paratype, an adult female 58 mm. in standard length, C.U., No. 8324 (for data see p. 5).

FIG. 2. *Hadropterus notogrammus:* side view of holotype, an adult male (for data see p. 5).

FIG. 3. *Hadropterus peltatus:* side view of an adult male, 65 mm. long, collected by E. C. Raney on May 14, 1938, in outlet of Spencer Lake, Susquehanna River system, 2 miles north of Spencer, Tioga County, New York.

FIG. 4. *Hadropterus maculatus:* side view of an adult male, 47 mm. long, collected by Raney and E. A. Lachner on April 2, 1940, in South Fork of New River, Kanawha River system, 1 mile southwest of Fleetwood, Ashe County, North Carolina.

All photographs by Art Smith.

PLATE I

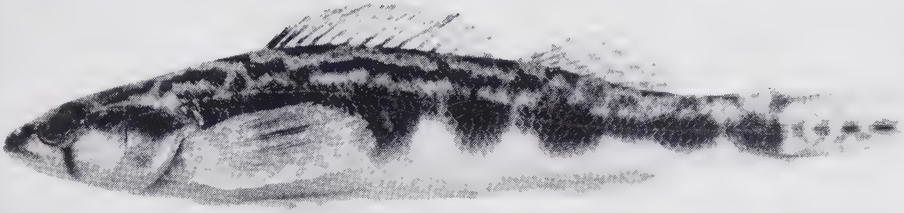

FIG. 1

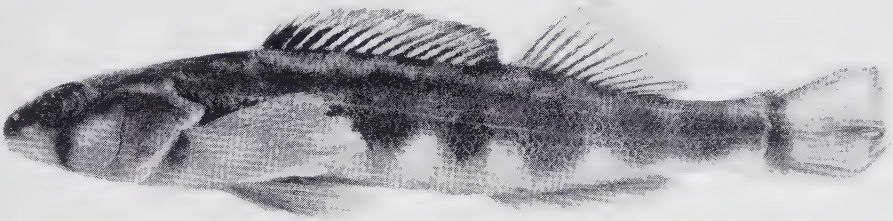

FIG. 2

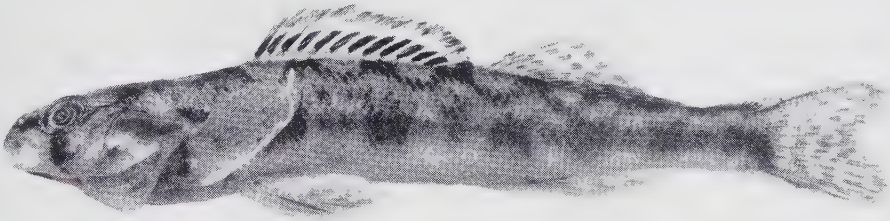

FIG. 3

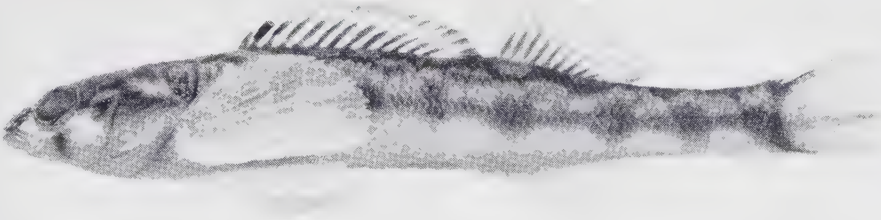

FIG. 4

PLATE II

Fig. 1. *Hadropterus notogrammus:* dorsal view of female specimen shown on Plate I, Fig. 1.

Fig. 2. *Hadropterus notogrammus:* dorsal view of holotype, an adult male.

Fig. 3. *Hadropterus peltatus:* dorsal view of adult male shown on Plate I, Fig. 3.

Fig. 4. *Hadropterus maculatus:* dorsal view of adult male shown on Plate I, Fig. 4.

All photographs by Art Smith.

PLATE II

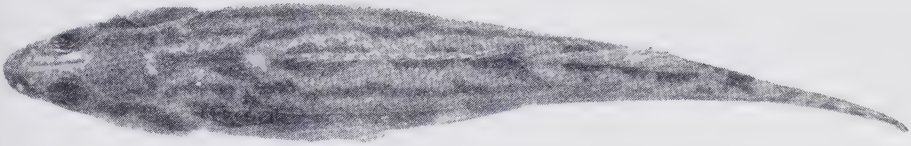

FIG. 1

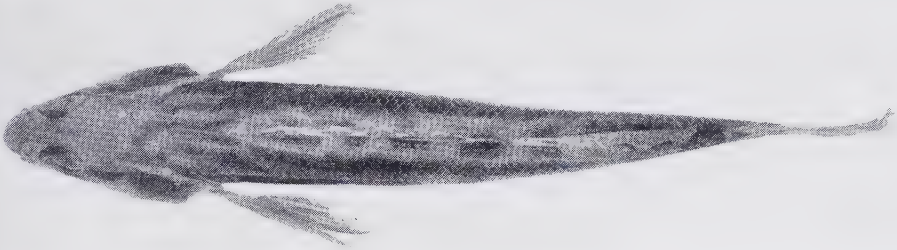

FIG. 2

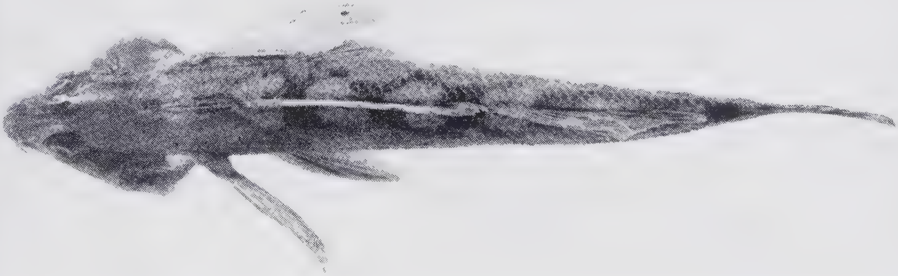

FIG. 3

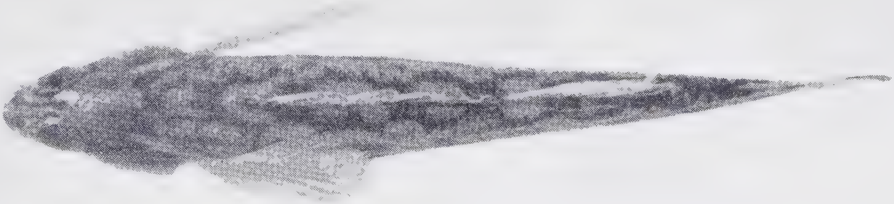

FIG. 4

Contribution No. 391

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An Instrument for Recording Ultra Low Frequency Ocean Waves*

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(Received May 13, 1948)

An instrument has been designed to measure low amplitude waves whose frequencies fall between those of the wind-generated ocean swell and those of the astronomic tides. Its maximum sensitivity is to waves whose period is 15 minutes, and its pass band extends approximately from 2-minute periods to 2 hours. The suppression of the ocean swell and tides (whose amplitudes are much greater than those of the waves to be studied) is accomplished by means of capillaries and air chambers which give the instrument a response characteristic analogous to that of an electrical $R-C$ circuit. Records obtained show the continual presence of waves in this previously unexplored portion of the spectrum of gravity waves in the sea.

INTRODUCTION

ES in a storm area form a most irregular ttern, covering a wide range of fre- Under typical conditions most of the concentrated, however, within a rela- rrow range of periods, say, from 5 to 9 After the waves leave the storm area el as *swell*. Selective attentuation of the periods leads to a gradual shift of the aximum toward the longer periods. The minent swell from a storm area several miles away has periods of 12 to 16 amplitudes of the order of 2 feet. The well period visually observed is 22 During the last few years a number of swell-recording instruments have been by British and American activities.[1] truments have demonstrated the exist- w long forerunners to the swell, with to about 30 seconds.

octaves lower on the frequency scale emidiurnal and diurnal tides caused by cting forces of the moon and sun. The des of the tides are of the same order of de as those of the swell. Automatic tide s have been in continuous operation for ears along most coastlines of the world.

The only waves that have been noticed of frequencies between those of the swell and tides are occasional *tsunamis*[2] caused by submarine earthquakes or eruptions. If waves of these frequencies occur commonly, their amplitudes must be small compared to those of the swell and tides.

The instrument described here is designed to cover the range in periods which is not adequately covered by either the tide or the swell recorders. The first model of such an instrument was designed by Mr. J. Frautchy and the senior author to set off an alarm in the event of tsunami waves. Subsequently it was learned that Commander C. K. Green, U.S.C. and G.S., was working on a warning instrument which was similar in principle, but simpler in design and further developed. Accordingly, our work on the alarm instrument was abandoned in favor of the present recording unit for research purposes.

DESCRIPTION OF INSTRUMENT

The instrument is located at the end of the Scripps Institution Pier, in La Jolla, California. A five-inch stand-pipe is mounted vertically along a pier pile (Fig. 1) with its open end fifteen feet beneath mean sea level. Most of the pipe is filled with a highly refined petroleum oil. The movement of the oil column is impeded by a capillary. The length of the oil column and the location of the capillary have been selected so that even during extreme tides and waves the capillary remains within the oil column, and no oil is

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ibution from the Scripps Institution of Oceanog- ew Series, No. 391. This work represents results h carried out for the Office of Naval Research, ographic Office, and the Bureau of Ships of the tates Navy Department under contract with the y of California.

itute of Geophysics, University of California, les, California.

itán de Corbeta (A.R.A.).

brief description and history of swell-recording nts see W. H. Munk, J. Met. 4, 46 (1947).

[2] Popularly known as *tidal* waves, although they bear no relation to the tide producing forces; observed periods of tsunami waves range from 10 to 70 minutes.

spilled into the sea. In standard tide gauges the pipe is filled with sea water and the restriction is placed at the bottom of the pipe. The present arrangement has the following advantages: (a) corrosion and fouling of the capillary is avoided; (b) the air in the reservoir is not in contact with water and can be kept reasonably dry; (c) distortion of the wave form by capillary end-effects is reduced by the use of a relatively viscous fluid.

An air chamber above the oil column is connected to an air reservoir, the volume of which can be readily adjusted. A fine capillary permits leakage of air between the reservoir and the atmosphere. The remaining part of the instrument consists of glass cylinders mounted above the deck level of the pier, and connected as shown in Fig. 1. The differential between the air pressure in the last glass cylinder and the atmospheric pressure actuates a strain gauge pressure transmitter, the output of which is recorded by a Leeds and Northrup Micromax located in one of the buildings ashore.

The capillary R_O' in the stand-pipe tends to
suppress any short period vertical oscillat
the oil column due to wind waves or swell. T
column does respond to the rise and fall
tides, but due to the leakage of air throug
air capillary R_A' this very slow movement
not lead to appreciable pressure changes i
air pocket above the oil column. The oil a
capillaries have therefore the characterist
low and high pass filters, respectively, an
pressure changes in the air pocket result r
from periods intermediate between those
swell and tides.

The glass cylinder assembly serves as addi
filter stages. The oil capillary connecting th
two glass cylinders suppresses the transmiss
short period waves to the second air rese
whereas the air capillary in the third cy
reduces pressure changes of long periods.
additional "stage" of the two cylinders th
the characteristics of a band pass filter, a
many stages can be attached as are requi
achieve the desired response characteristic
present instrument consists of one glass cy

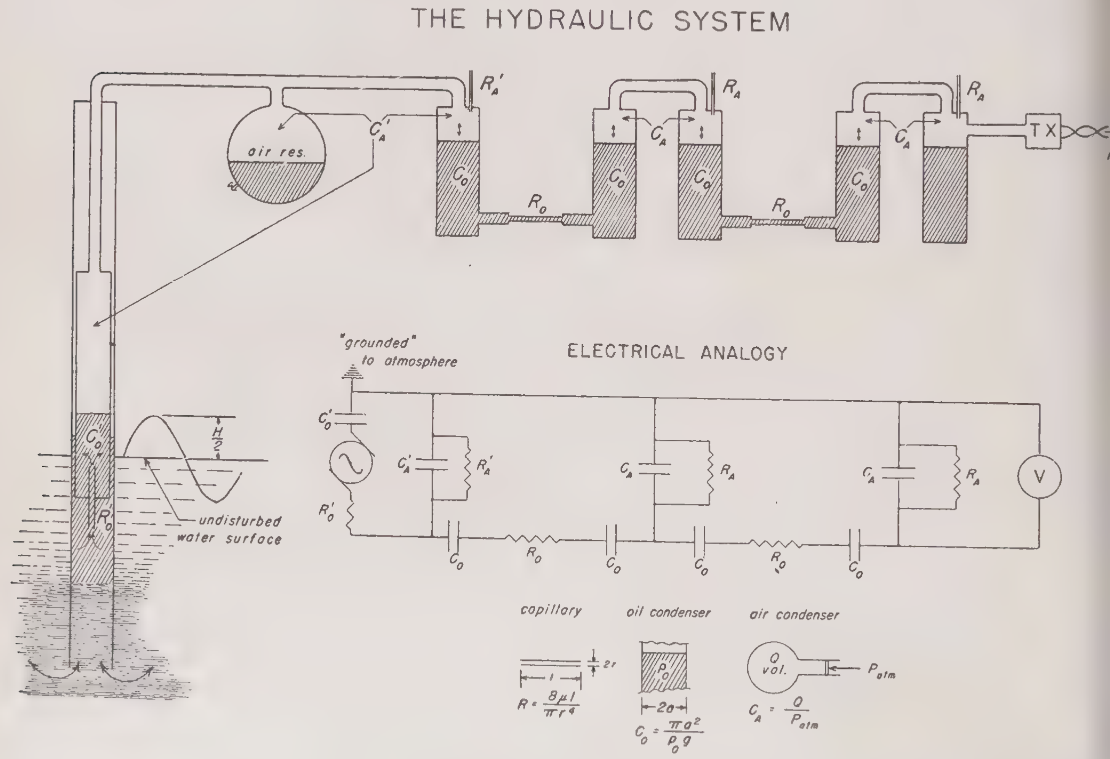

FIG. 1. Schematic presentation of the low frequency wave instrument and the electrical analogy which has eq
response characteristics. Resistances and condensers in the electrical circuit are drawn either to the right or
beneath the analogous hydraulic unit.

. I. Numerical values of circuit constants.

esistances (cm^{-4} sec.$^{-1}$)	Capacitances (cm^4 sec.^{2} g^{-1})
= 1,090	$C_O' = 0.132$
= 1,210	$C_A' = 0.119$
= 3,130	$C_O = 0.0915$
= 125,000	$C_A = 0.00115$

ddition to the main stand-pipe stage. A ass cylinder is provided to facilitate nt of the volume of air, C_A.

RESPONSE CHARACTERISTICS

nstrument is analogous to the $R-C$ shown in Fig. 1. The impressed e.m.f. nds to the pressure fluctuation at the f the stand-pipe due to the oscillation in . The output voltage is analogous to the ure in the last glass cylinder. The rate of flow of oil is analogous to the electric The resistance of the capillaries to flow air, which is analogous to current resist- iven by Poiseulle's law:

$$R = (8\mu l/\pi r^4), \qquad (1)$$

is viscosity, l and r the dimensions of the (Fig. 1). The rise in oil level in a al vessel of radius a is analogous to the of a condenser of capacitance

$$C_O = (\pi a^2/\rho_O g), \qquad (2)$$

is the oil density, and g the acceleration gravity. The compression of air in a of volume Q and pressure P is analogous arging of a condenser of capacitance

$$C_A = (Q/P)(1-k), \qquad (3)$$

$=0$ corresponds to isothermal conditions -0.286 to adiabatic conditions. Computa- how that for long period waves quasi- mal conditions will be encountered; fur- ore, that the amplitude of the pressure tions are small compared to the mean re ($P_{\text{atmos.}}$), and the amplitude of the fluctuations small compared to the mean ume. Therefore, $C_A = Q/P_{\text{atmos.}}$, and may en as constant.

the prime (′) designate the characteristics first stage (stand-pipe and first cylinder), t all subsequent stages (2 cylinders each) be identical. Let the subscript "O" refer to oil and "A" to air. The periods of minimum attenuation of the first stage, and of subsequent stages, are given by

TABLE II. Smallest detectable wave amplitude in cm for waves of stated period.

Number of filter stages	Swell average 12^s	long 18^s	Working range short 2^m	resonance 15^m	long 2^h	Tides semi-diurnal 12^h	diurnal 24^h
1	10.9	6.45	1.14	.455	1.12	6.45	14.2
2	25.0	11.2	1.36	.481	1.35	11.0	39.0
3	66.5	26.5	1.60	.528	1.60	26.3	131

$$T_o' = 2\pi C_O' R_A' (\beta'\gamma')^{\frac{1}{2}},$$
$$T_o = 2\pi (C_O/2) R_A (\beta\gamma)^{\frac{1}{2}}, \qquad (4a, b)$$

respectively, where

$$\beta' = (R_O'/R_A'), \quad \beta = (R_O/R_A),$$
$$\gamma' = (C_A'/C_O'), \quad \gamma = (C_A/C_O/2). \qquad (5)$$

Let T denote wave period, A the amplitude of the impressed pressure fluctuation at the bottom of the stand-pipe, and A_P the amplitude of the air pressure fluctuation in the last stage. For the long waves recorded by the instrument, A is equal numerically to the amplitude of the waves at the sea surface. It follows from standard methods of circuit analysis that the amplitude response A_P/A and the phase angle θ equal, respectively, the modulus and argument of a complex response function Δ. For one, two, or three stages $\boldsymbol{\Delta}$ is given by

$$\boldsymbol{\Delta}^{-1} = 1 + \alpha',$$

$$\boldsymbol{\Delta}^{-1} = 1 + \alpha' \left[1 + \frac{R_A'}{R_A} + \alpha \right] + \alpha,$$

$$\boldsymbol{\Delta}^{-1} = 1 + \alpha' \left[1 + 2\frac{R_A'}{R_A} + \alpha\left(3 + \frac{R_A'}{R_A}\right) + \alpha^2 \right] + 3\alpha + \alpha^2, \qquad (6)$$

where

$$\alpha' = (\beta' + \gamma') + i(\beta'\gamma')^{\frac{1}{2}} \left(\frac{T_o'}{T} - \frac{T}{T_o'} \right),$$

$$\alpha = (\beta + \gamma) + i(\beta\gamma)^{\frac{1}{2}} \left(\frac{T_o}{T} - \frac{T}{T_o} \right). \qquad (7)$$

In order for the instrument to have effective cut-off characteristics, the periods for maximum response in the various stages should be equal, or

$$T_o' = T_o. \qquad (8)$$

Because of the dissipative nature of the circuit, each additional stage lowers the response in the pass band. To minimize this effect we note that at maximum response $(T = T_o)$

$$\alpha' = \beta' + \gamma', \quad \alpha = \beta + \gamma,$$

and in order for the modulus of Δ to be large, $(\beta' + \gamma')$ and $(\beta + \gamma)$ must be small. On the other hand, for swell $(T \ll T_o)$ and tides $(T \gg T_o)$,

$$\mathrm{mod}(\alpha') \propto (\beta'\gamma')^{\frac{1}{2}}, \quad \mathrm{mod}(\alpha) \propto (\beta\gamma)^{\frac{1}{2}},$$

and in order for Δ to be small, $\beta'\gamma'$ and $\beta\gamma$ must be large. These conditions are most nearly fulfilled if

$$\beta' = \gamma', \quad \beta = \gamma. \qquad (9a, b)$$

Another condition is imposed by the requirement that the response should as far as possible be independent of the stage of tide. Let $\Delta Q'/Q' = n$, where $\Delta Q' = \pi(a')^2 A_t$ is the amplitude of the volume fluctuation due to tidal oscillation of amplitude A_t. It follows from (2), (3), and (5) that

$$\gamma' = (\rho o g A_t / n P_{\text{atmos.}}); \qquad (10)$$

for $n = 0.1$ and $A_t = 100$ cm, $\gamma' = 0.9$.

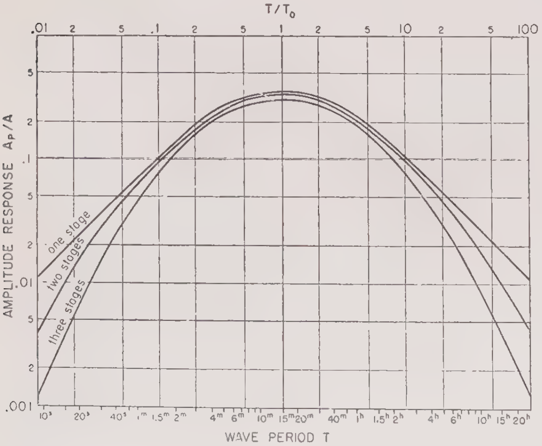

FIG. 2. Response characteristics expressed as ratio between the amplitude A_P of the air pressure fluctuation in the last stage, and the amplitude A of the impressed pressure fluctuation at the bottom of the stand-pipe.

A maximum response period of

$$T_o = 15 \text{ minutes}$$

was chosen because it lies halfway, on a rithmic scale, between the longest swell shortest tide. In order for $A_P/A \geqslant 0.1$ ov band width $(1/8) \leqslant T/T_o \leqslant 8$, or approxim $2^m \leqslant T \leqslant 2^h$, one obtains

$$\beta = 0.025.$$

Numerical values of the eight circuit const are given in Table I. Equations (4), (8)- impose six conditions upon these const leaving two degrees of freedom; these were termined by the diameters of the stand-pipe and of the glass cylinders (10 cm).

The response characteristics are show Figs. 2 and 3. Full deflection of the rec corresponds to a pressure amplitude of 6 inch sea water. The scale is divided into 100 s visions, one of which is approximately the sma detectable amplitude of pressure fluctua Table II gives amplitudes of waves in the o for various periods corresponding to this r mum detectable amplitude on the record.

INSTRUMENT DIMENSIONS

Poiseulle's law (Eq. (1)) gives the resistan of the capillaries related to the viscous prope of the fluids. Associated with the inertial p erties of the fluid, capillaries also offer resist R_i which can be computed according to the

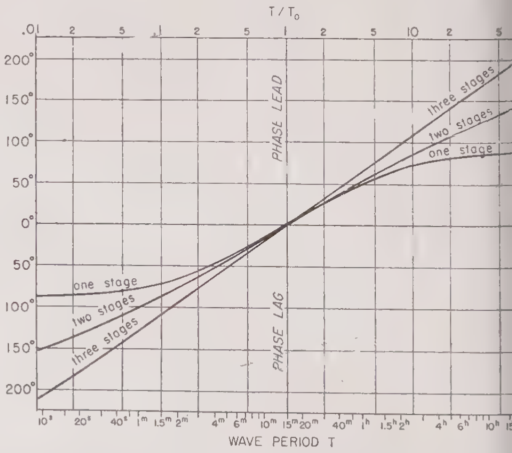

FIG. 3. Phase difference between air pressure fluct in last stage and impressed pressure fluctuation a bottom of the stand-pipe.

BLE III. Dimensions of the instrument.

	Description	First stage (′)	All other stages
nd lers	radius a (cm) air volume Q_A (cm^3)	6.35 1.19×10^5	5.00 1.14×10^3
s	radius r_O (cm) length l_O (cm)	0.40 11.0	0.30 10.1
s	radius r_A (cm) length l_A (cm)	0.050 17.2	0.0125 6.70

g the flow through orifices:

$$R_i=\frac{\rho(gh)^{\frac{1}{2}}}{\sqrt{2}\pi r^2 C_D}, \tag{13}$$

s the pressure head and C_D the discharge t which depends upon the design of the and the Reynolds' number of the flow. rison of Eqs. (1) and (13) gives

$$l=\frac{1}{8\sqrt{2}C_D}\left(\frac{R_\mu}{R_i}\right)(gh)^{\frac{1}{2}}\frac{\rho}{\mu}r^2.$$

ependence of R_i on h indicates a non-sponse and thus an undesirable distortion s the capillary resistance is related to effects. Within the response range of the nt the pressure head is not likely to 0 cm of sea water. Setting $h=10$ cm, $R_i/R_\mu=0.15$, and $\rho_O=0.875$ g cm^{-3}, g cm^{-1} sec.$^{-1}$ for oil, $\rho_A=1.25\times10^{-3}$ $_A=1.7\times10^{-4}$ g cm^{-1} sec.$^{-1}$ for air, gives

$$l_O=67r_O{}^2, \quad l_A=465r_A{}^2$$

minimum capillary length (cm) corre- to a capillary radius r (cm), in order for al resistance to be less than 15 percent of ous resistance. Equations (14) and the of the circuit constants (Table I) es- determine the dimensions of the instru- ee Table III).

DISCUSSION

The instrument responds to fluctuations in atmospheric pressure, but under ordinary circumstances these are too small to be troublesome. The response characteristics vary somewhat with temperature as a result of changes in the viscosity of oil and air. Fortunately, the coastal air temperature in the San Diego region fluctuates within narrow limits, the average ranges in diurnal and seasonal temperature being 5°C and 15°C, respectively. The instrument itself is well sheltered from sunlight and wind.

The response characteristics have been checked in three ways: (a) by comparison of the computed and recorded amplitudes and phase angles of the semidiurnal tides. This test was carried out for the first stand-pipe stage only, and for the stand-pipe and glass cylinder stages combined; (b) by comparison of the computed and observed amplitudes and phase angles of a well defined swell; (c) by a square wave test, involving controlled pressure fluctuations in the air reservoirs of the stand-pipe stage. In all instances computations based on the design parameters agreed with the observed results within the limits of observational error.

Records obtained with the instrument reveal a complex system of waves covering the entire frequency range of the instrument. To assist in the analysis of these records a magnetic tape recorder is being adapted to a very slow recording speed. Play-back at about 10^5 times the recording speed will bring the frequencies into the sonic range, where a spectrum analysis can be accomplished by existing equipment.

ACKNOWLEDGMENT

We are indebted to Dr. Carl Eckart for his interest and many suggestions.

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ADJUSTMENT OF BIKINI ATOLL TO OCEAN WAVES

Walter H. Munk and Marston C. Sargent

(Contribution from the Scripps Institution of Oceanography, New Series, No. 392)

Abstract--Atolls in the trade-wind belt withstand a continuous heavy pounding from ocean waves. Against the windward side of Bikini Atoll alone it is estimated that waves dissipate 500,000 hp, one-fourth the power generated at Hoover (Boulder) Dam. To withstand these forces the exposed reefs are moulded into a most effective natural breakwater, consisting of long narrow grooves in the seaward face of the reef, and surge channels on the reef flat. These surge channels are tuned to the prevailing wave periods. Their distribution around the reef conforms to the distribution in wave activity, which in turn is controlled by prevailing winds over the North and South Equatorial Pacific.

Some of the power of the breaking waves is utilized to maintain a water level just inside the surf zone about 1.5 ft above the general sea level. The water flows downhill over the reef into the lagoon, regardless of the stage of the tide, with an average speed of 0.5 to 1.0 knot, but occasionally with speeds up to four knots. The reef as a biological community utilizes this current and maintains thereby a wave-resisting and modifying structure.

Grooves and surge channels--The features to be described here are best developed between kini and Amen Islands (see Fig. 1), where the reef is directly exposed to the waves of the pre- ling trade winds [EMERY, TRACEY, and LADD, in press]. Grooves cut the seaward face of reef at fairly regular intervals (see Fig. 2) and give it the appearance of a series of buttresses sing from the debris-covered slope of the atoll.

The grooves commence at a depth of 50 to 75 ft, then run steeply up the reef slope into and ough the surf zone. At the inner end, they may end abruptly or be continued as surge channels, as tunnels, with blowholes, under the reef platform. Just inside the surf zone, around the blow- es and the heads of grooves and channels, nullipores and coral colonies rise about two ft above general reef level. The upper faces of the buttresses are paved with living nullipores which sent an extremely rough surface. The sides of the grooves are covered with projecting, often cket-like, colonies. The bottoms of the grooves consist of relatively smooth rock and sand.

Between Bikini and Amen Islands the grooves are spaced about 25 ft apart, are about 16 ft ep at their inner ends, and vary in width from three to six ft. The grooves play a vital part in function of the coral reef as a breakwater. Near their outer ends, which extend to the maxi- m depth of appreciable wave action (see Appendix 1), they interfere with the normal orbital er motion associated with waves on a sloping bottom, by taking the bottom out from under the ves; at the inner end they pursue a divide and conquer policy. The resulting effect on waves is markable. To an observer standing on the platform just inside the surf zone, the breakers ap- r to come crashing down upon him; two sec later, the wave has virtually disappeared, its mentum converted into a noisy surge which rushes up the channels on each side of the platform. ch of the remaining energy is spent when the surge meets the backrush from the preceding eaker. Wave energy is also dissipated by friction along the sides of the grooves and channels, here an abundant bracket-like growth of organisms is found.

The surge channels are properly tuned to the average wave characteristics (see Fig. 2). An verage depth of 15 to 20 ft, and a length of about 200 ft (ℓ_1 in Fig. 2) between the outer end of the latform (Lithothamnion ridge) and the inner ends of the channels correspond to a fundamental eriod of oscillation of eight sec, which is also the prevailing period of the waves of the trade inds (see Appendix 2). As a result, the uprush of each wave will meet the backrush of the pre- eding wave at approximately mid-channel.

Distribution of grooves and prevailing wave directions--The dimensions of grooves around the ntire reef of Bikini Atoll were estimated from aerial photographs, and are designated by arrows n Figure 1. The spacing s, width w, and outer length ℓ_0 (see Fig. 2) of the grooves are designated y the spacing, width, and length of the arrows. Photographs of the reef to the south of Bikini Island ere unsuitable for the determination of the grooves, but it is known that grooves are well developed n that area.

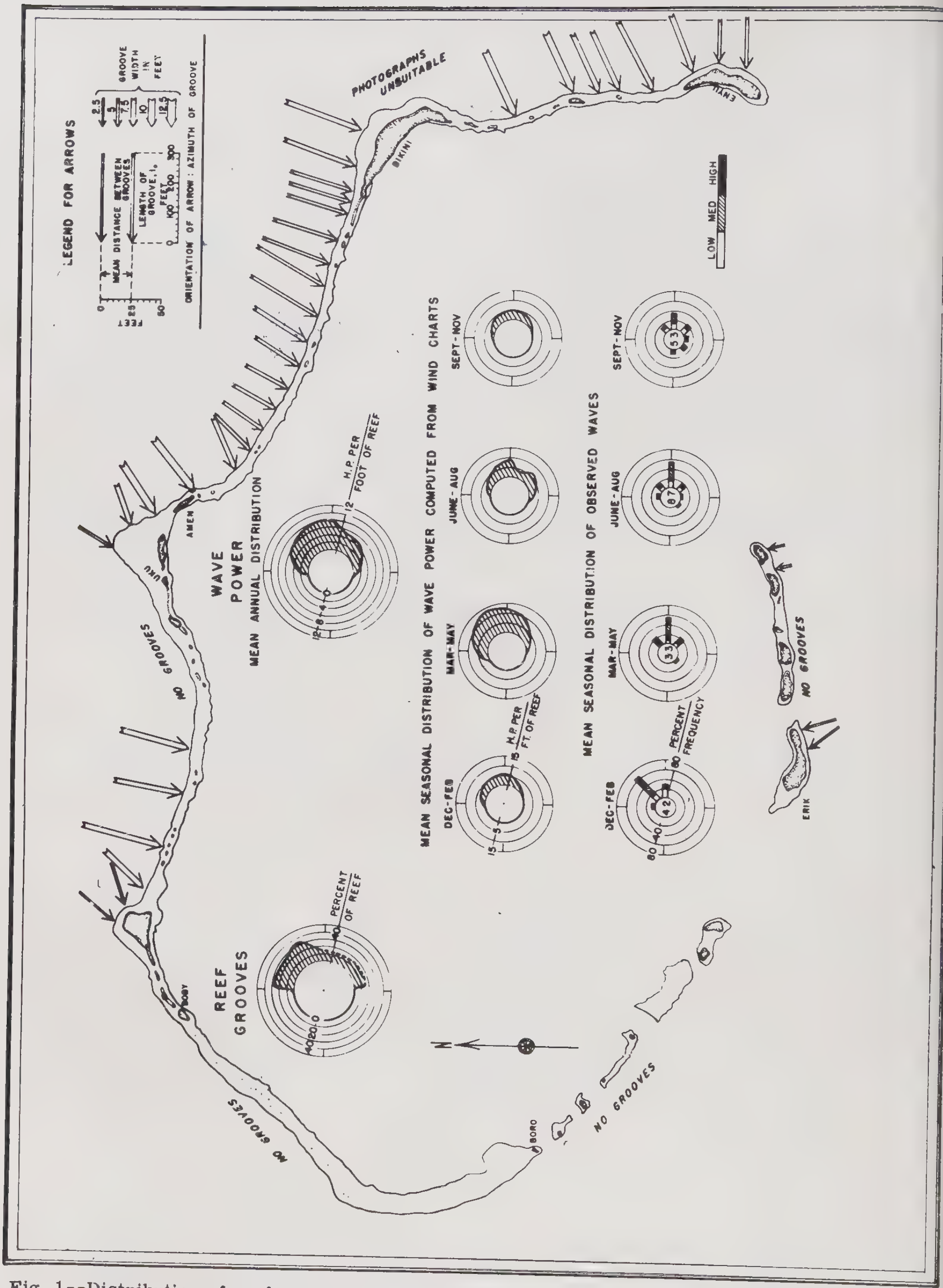
LEGEND FOR ARROWS
MEAN DISTANCE BETWEEN GROOVES
LENGTH OF GROOVE, l, FEET
FEET
0
25
50
100
200
300
GROOVE WIDTH IN FEET
2.5
5
7.5
10
12.5
ORIENTATION OF ARROW: AZIMUTH OF GROOVE
PHOTOGRAPHS UNSUITABLE
ENYU
BIKINI
AMEN
UKU
NO GROOVES
ROBY
BORO
ERIK
WAVE POWER
MEAN ANNUAL DISTRIBUTION
H.P. PER FOOT OF REEF
12
8
4
0
MEAN SEASONAL DISTRIBUTION OF WAVE POWER COMPUTED FROM WIND CHARTS
DEC-FEB
MAR-MAY
JUNE-AUG
SEPT-NOV
H.P. PER FT. OF REEF
15
5
MEAN SEASONAL DISTRIBUTION OF OBSERVED WAVES
PERCENT FREQUENCY
80
40
42
33
87
53
LOW
MED
HIGH
REEF GROOVES
PERCENT OF REEF
40
20
0
N

Fig. 1--Distribution of reef grooves and wave power around the reef of Bikini Atoll; the length, width, and spacing of the grooves are proportional to the length, width, and spacing of the arrows drawn against the reef; polar coordinate graph to the left shows per cent of area occupied by grooves as function of their exposure; polar coordinate graphs to the right show mean distribution of computed wave power, and of observed waves

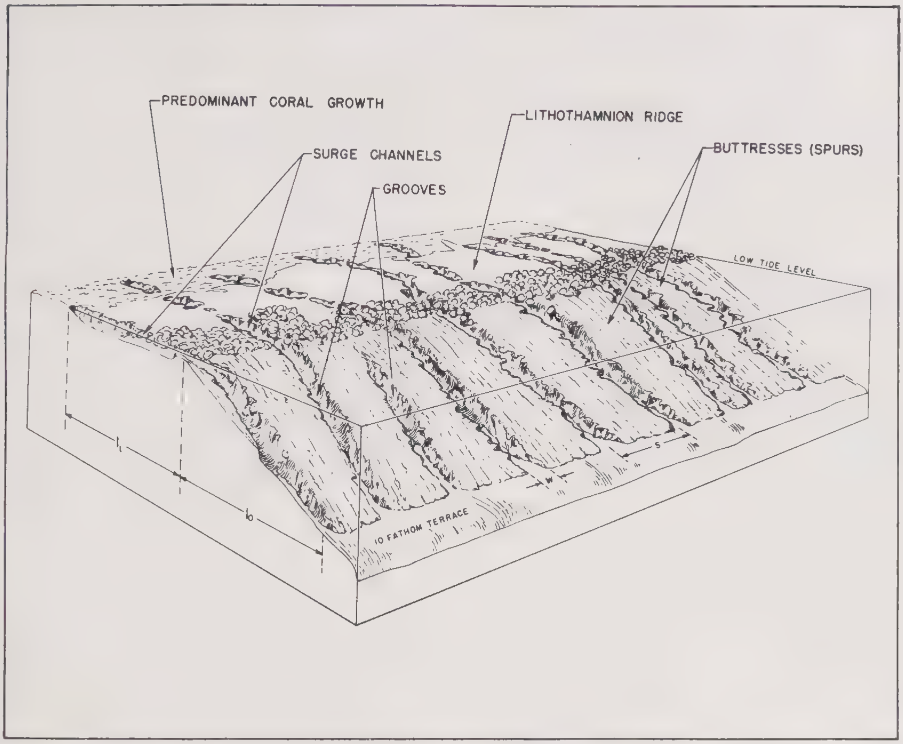

Fig. 2--Generalized sketch of seaward face and top of reef on windward side of Bikini Atoll; original by D. B. Sayner

The greater length of the grooves with northern exposure relative to those with southern posure is due to the steeper slope of the reef to the south [EMERY, TRACEY, and LADD, in ess]. The absolute depth at which the grooves commence appears to be approximately constant, d to extend to the greatest depth for which wave action is appreciable (see Appendix 1).

The per cent of reef area occupied by the grooves equals 100 w/s. This is plotted as a function the azimuth of the grooves on the polar coordinate graph on the left in Figure 1. No grooves were und where the reef exposure has a westerly component.

The distribution of grooves can be correlated with the distribution of wave power around the oll. The polar coordinate graphs to the right in Figure 1 give the average seasonal and annual stribution of wave power plotted against reef exposure and expressed in units of hp per foot ngth of reef.

Wave power was computed in the following manner. The principal generating areas were determined from the Atlas of Climatic Charts of the Oceans [UNITED STATES WEATHER BUREAU, 938]; they fall into the trade-wind belts of the North and South Pacific. (Swell from the "roaring rties" may occasionally reach the northern Marshalls, but will be too low to be significant.) The frequencies of the prevailing winds in the two main generating areas, and of winds from other directions, were determined from wind roses on the North and South Pacific Pilot Charts. The height, period, and direction of waves reaching Bikini from all directions were then computed, llowing the method for forecasting sea and swell from weather maps [SVERDRUP and MUNK, 1946a]. Finally the bending of waves around the Atoll due to refraction was estimated [SVERDRUP and MUNK, 1946b] and the wave power computed (see Appendix 3).

A rough check of the validity of these computations could be obtained from sea and swell observations appearing in the Sea and Swell Charts, Northwestern Pacific (Hydrographic Office 10712C). Averages were formed for each season, taking into account all observations in the area between longitudes 160°E to 170°E, and between latitudes 5°N to 15°N. These are presented by the wave roses in Figure 1. The main features in the observed wave distribution are in agreement with the computed distribution of wave power.

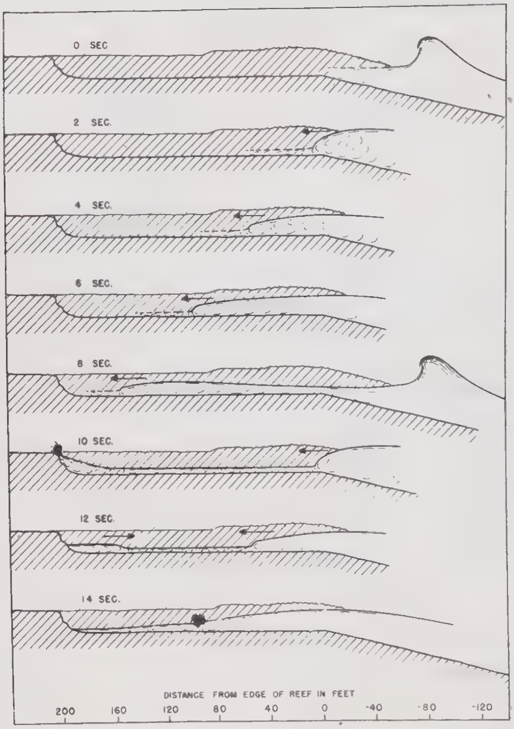

Fig. 3--Breaking wave produces surge which travels up the surge channels, is reflected on the upper end, and meets surge from subsequent breaker mid-channel; surge channels are tuned to the period of prevailing waves

The graph of the annual distribution of wav power is based entirely upon the computed rath than the observed wave characteristics, partly cause of the small number of observations, but chiefly because the quality of these observation is believed to be inferior to the quality of the computed values.

The diagrams in Figure 1 show a significa correlation between the directional distribution of wave power and of reef grooves. Grooves a restricted to reefs with a component of exposu to the east, the direction from which wave action is pronounced. Due to wave refraction a small portion of the wave power does reach the western sides of the Atoll, but there the power dissipated amounts to only a fractional hp per foot length of reef, and it appears that at least one or two hp is required for the development of grooves. On the eastern half of the reef the average power delivered by the waves equals three hp per foot length of reef, or about 20 hp per groove.

The distribution of grooves reveals a maximum for an east-northeast exposure, and a secondary maximum for southeast exposure. These features are associated with the princip wave-generating areas in the trade-wind belts of the North Pacific and South Pacific, respectively. The distribution of wave power reveals the same features; except during the summer months the effect of the distant South Pacific trade winds is overshadowed by the effect of th local trade winds. For a corresponding locati in southern latitudes the reverse should be tru and the distribution should be a mirror image of the one found at Bikini.

The bimodal distribution of grooves points strongly toward a wave origin; if the channels we to be attributed to direct wind action, the development in the southeast quarter would be missing.

Head of water at reef edge--Not all the energy of the incoming waves is dissipated by frictio Some energy is converted into potential energy to maintain a water level at the outer edge of the reef at about two ft above the mean water level of the ocean and lagoon water. If the entire wave energy were to be consumed in lifting the water which flows over the reef, the level of this volum of water could be maintained 42 ft above the mean sea level (see Appendix 3). Therefore only abo 5 per cent of the wave's energy is utilized to raise the water level, and 95 per cent is dissipated friction, a large part of it within the surge channels.

It may be worthwhile to consider the design of artificial breakwaters along the lines of the natural coral reef breakwater, as the present structure of these reefs represents the result of thousands of years of adaptation resulting in a most suitable structure to withstand the wave forc Artificial surge channels have indeed been employed on the south coast of the Mediterranean in th generation of electricity by means of wave power. These channels were relatively wide at their outer end and converged gradually toward the inner end. In this manner the water level in a reservoir was maintained at an average elevation of 40 ft above the mean sea level.

Wave-driven currents over the reef--From the region of maximum elevation the current flo into the lagoon under the influence of gravity assisted by wind traction. Between Bikini and Amer Islands, the speed is about one ft/sec; except during spring low tides, when the retarding effect o bottom friction is disproportionally large, this speed is remarkably independent of tide. In the presence of obstructions the wave-driven current may give rise to striking features. For examp a few days after the arrival of the USS Bowditch a 100-ft channel broke through the sandspit at th northwest end of Bikini Island, and water flowed through this channel in a steady stream for almo six months.

Currents over the reef were measured by dropping dye bombs from planes, and taking timed ographs of the drifting color patches [VON ARX, 1948]. Between February and April 1946, e the trade winds blew predominantly from the east-northeast, wave-driven currents flowed the lagoon over the entire eastern and northern reefs, adding 3×10^{14} cm^3 of water, one per of the entire lagoon volume, during each 12-hourly interval. During an equal time interval tidal flow (chiefly through the deep southwesterly passages) amounted to two per cent of the on volume. Although the oscillating tidal current represented the principal component of water ange between the ocean and the lagoon, the one-directional wave-driven current is of primary ortance to the renewal of water in the lagoon. The latter feature was of interest with regard e flushing of the lagoon of radioactive water.

The wave-driven current is important also for another reason. At noon, expecially during low , the water over the reef becomes warmer, more saline, and supersaturated with oxygen. Upon ering the lagoon, this "reef water" may be recognized as a distinct water type. The mixing of water with the lagoon water provided a method for computing the rate of vertical diffusion NK, EWING, and REVELLE, in press].

Discussion and conclusions--Waves breaking over coral reefs may lead to the formation of oves and to the flow of currents over the reef. The only other known examples of currents due wave action are longshore currents and rip currents caused by waves breaking on gently sloping ches [MUNK and TRAYLOR, 1947]. Since the waves represent an integrated effect of the winds, r energy being accumulated during many hours, and over thousands of miles, a wave-driven rent assures a steadier supply of water than a wind-driven current.

The waves and the wave-driven current may be of biological significance in three ways. First, y limit luxuriant growth of Lithothamnion and other encrusting coralline algae to situations ex- ed to the heaviest wave action, possibly because such action prevents the establishment of sed- ary organisms. Secondly, the current maintains a nearly constant supply of mineral nutrients dissolved gases over the whole width of the reef. Thirdly, as noted above, the current carries er into the lagoon, which at noon is supersaturated with oxygen. Also, on the basis of evidence ented elsewhere [SARGENT and AUSTIN, in press], it is believed that there is a net trans- t of organic matter into the lagoon which is of importance in the total organic matter get of the lagoon.

Appendix 1

This work represents results of research carried out for the Hydrographic Office, the Office aval Research, and the Bureau of Ships of the Navy Department under contract with the Uni- rsity of California. The original of Figure 2 was drawn by D. B. Sayner.

Depth of wave action--The average speed of water movement along the bottom in water of depth given by

$$u = 2\pi H/T \sinh^{-1} (2\pi h/L) \ldots\ldots (1)$$

re H and T are the height and period of the wave responsible for the water movement. The wave th is given by

$$L = (gT^2/2\pi) \tanh (2\pi h/L) \ldots\ldots (2)$$

re g is the acceleration due to gravity. For a wind speed of 16 knots, blowing over a long fetch for a long time, the wave height and period equal seven ft and eight sec, respectively [SVER- RUP and MUNK, 1946a]. These figures are in agreement with the observed dimensions of trade- nd waves. Simultaneous solution of (1) and (2) leads to the numerical values shown in Table 1.

able 1--Mean orbital speed on the ocean bottom

Depth h	Speed u	Size of particles which can be eroded
ft	ft/sec	mm
50	1.2	3
75	0.8	1
100	0.5	0.05
125	0.32	No erosion

The outer ends of the grooves fall into a depth of about 75 ft, where the average speed due to wave action is about 0.8 ft/sec. The third column shows the size of particles which can be eroded by a current of speed u, based upon measurements in rivers by Hjulström [TRASK, 1939, pp. 10-11]. According to Hjulström, "...fine sand, which has a diameter of 0.3 to 0.6 mm, is the easiest to erode, whereas both silt and clay on the one hand and coarse sand and gravel on the other require higher velocities.'' If these conclusions are applicable here they indicate that no erosion can take place for current speeds less than 0.5 ft/sec, that is, at depths exceeding 100 ft, no matter how small the size of the grains.

Appendix 2

At the depth of 75 ft the reef slope is relatively gentle, forming virtually a terrace [EMERY, TRACEY, and LADD, in press]. One would be tempted to ascribe this ''ten-fathom terrace'' to wave action, were it not for the fact that it is also found inside the lagoon.

Table 2--Length of channels for maximum interference

Period T	Length l_2
sec	ft
6	130
8	175
10	220

Dimensions of surge channels--The speed of a surge in a channel equals approximately $\sqrt{gh}$, where h is the depth of the water measured from the highest point in the surge. For effective interference the surge must travel a distance of roughly the length of the channel during one wave period (see Fig. 3). The corresponding length of the channel equals approximately $T\sqrt{gh}$. Setting $g = 32.2$ ft/sec^2, $h = 15$ ft, leads to the values shown in Table 2.

Appendix 3

The wave period in the region of the northern Marshalls is remarkably constant and falls within the limits of seven to nine sec, probably more than 90 per cent of the time. Over most ocean areas the period of the significant waves vary between such wide limits (probably six to 14 sec) that resonance for any permanent structure would be achieved only a small fraction of the time.

Wave power--The mean energy dissipated by the waves each sec against a unit width of reef is $(1/32\pi)\,\rho g^2H^2T$ where ρ is the density of water. The transport of water per ft width of reef equals $h'V$ where h' is the depth of water over the reef, V the corresponding speed of flow. If the entire wave energy were to be utilized in raising the water flowing over the reef, then

$$(1/32\pi)\rho g^2H^2T = \rho g\, h'Vs \quad \dots\dots\dots\dots$$

so that the vertical distance through which the water would be raised is

$$s = gH^2T/32\pi h'V \quad \dots\dots\dots\dots$$

Setting $H = 7$ ft, $T = 8$ sec, $h' = 3$ ft, $V = 1$ ft/sec gives $s = 42$ ft.

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Contribution No. 393

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"LEAPFROGGING" BY TOPSMELT AND SHARK[1].—The two observations reported here supplement those accumulated by Gudger (Fishes That Play "Leapfrog," Am. Nat., 78, 1944: 451–463, fig. 1). Obviously it is not uncommon for fishes to leap repeatedly over a floating object. Whether this action serves to remove ectoparasites or merely to provide an outlet for exuberant spirit—or both—are queries that come to mind.

The leaping may be compared with a habit very often displayed by many bottom fishes (and whales), namely the scraping of the sides against rocks and other submerged objects. That habit is ordinarily supposed to serve in the removal of ectoparasites.

On May 24, 1948, a calm day, with a group of colleagues at the end of the Scripps Institution pier near La Jolla, California, I observed fish engaging in this spectacular show. Repeatedly, for about one-fourth hour, one to several fish 6 to 9 inches long leaped over a floating stick about 2 × 15 inches. They usually went across the middle of the stick at right angles to its long axis. Sometimes they leaped clear; on other jumps they scraped their bellies or sides against the board, but they always went over. The urge seemed to be contagious, for the action was frequently repeated and once, toward the end of the performance, about 10 fish leaped in close succession, occasionally 2 at a time. After the whole group passed in one direction, one made a leap in the reverse direction. Thereafter, except for one skip over some floating strands of surfgrass (*Phyllospadix*), no further leaping was observed, despite the fact that the aggregation of fish involved remained near the surface. A smaller stick that was thrown in was similarly ignored. The habit had not previously been observed here although fish of the same subspecies had very often been observed at and near the surface about the same place, both during the day and while night-fishing with a strong light.

All the leapfrogging fish observed on this occasion (with the aid of binoculars) appeared to be adult kelp topsmelt, *Atherinops affinis cedroscensis* Hubbs. Like several other leapfrogging fishes reported by Gudger, this species is a member of the family of silversides, the Atherinidae. These and the other kinds reported to leap over floating objects ordinarily swim at or near the surface.

While we were watching the atherines leap over a stick, John D. Isaacs, of Scripps Institution, recalled having once seen a somewhat similar performance. In August, 1943, he watched a shark about 7 feet long as it leaped onto and then slid over a corrugated paper box, floating in the ocean about 60 miles off the mouth of Columbia River. After a half-dozen leaps the box was broken and the action ceased. Isaacs thought that the species was the great blue shark, *Prionace glauca* (Linnaeus), which is not uncommonly encountered at the surface in that vicinity. This identification is in line with expectation. Thus a surface-swimming shark may be added to the list of surface-swimming teleosts that leap onto and over floating objects. I am grateful to Isaacs for permission to report this observation.—CARL L. HUBBS, *Scripps Institution of Oceanography, University of California, La Jolla, California.*

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 393.

Contribution No. 394

Yosemite Nature Notes

THE MONTHLY PUBLICATION OF
THE YOSEMITE NATURALIST DIVISION AND
THE YOSEMITE NATURAL HISTORY ASSOCIATION, INC.

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THE NATIVE FISH FAUNA OF YOSEMITE NATIONAL PARK AND ITS PRESERVATION[1]

By Carl L. Hubbs, Scripps Institution of Oceanography and
Orthello L. Wallis, Ranger Naturalist, 1948

Except for some studies and stories on the trout, the fish fauna of Yosemite National Park has been made known in only four publications. The first, a book by J. M. Hutchings, "In the Heart of the Sierras" (1886), contained a very brief statement on the fish life of the Merced River. The second was a chapter on "The Fishes of Yosemite National Park," by Barton Warren Evermann, in Ansel F. Hall's "Handbook of Yosemite National Park" (1921). The third was a brief treatise on "Fish and Fishing in Yosemite National Park," written by H. C. Bryant and included in "Yosemite Ranger Naturalist Manual" (1929). The fourth and most important was a pamphlet entitled "Fishes of Yosemite National Park." It was prepared by Willis A. Evans, as a result of observations that he made while serving as Ranger Naturalist in 1941, and it was issued as Volume XXIII,, Number 1, of **Yosemite Nature Notes** (1944). The paucity of reports on the fishes of Yosemite contrasts glaringly with the thorough treatment of the terrestrial vertebrates and reflects the limited study that has been made of the underwater life in this and other National Parks.

PRESERVATION OF THE NATIVE FISH FAUNA

The aquatic life of the National Parks has been much neglected, not only in research but also in the nature-preservation program (Madsen, 1937, pp. 395-397; Hubbs, 1940, pp. 3-4; Cahalane, 1947, pp. 69-70; Hubbs and Lager, 1949, pp. 98-99). The animal life above the water surfaces in the Parks has traditionally been treated as a sacred trust, to be preserved in strictly natural condition. That which lives below the water surfaces, in contrast, has commonly been managed as a recreational asset. Hunting of course is strictly prohibited, but fishing is generally allowed and is frequently encouraged. Only indigenous species are regarded as proper in the terrestial communities, and exotics are eradicated wherever possible. In contrast, exotic fishes, especially trouts, have frequently been stocked and maintained to provide sport in Park waters. The introduced species no doubt greatly disturb natural conditions in several ways: disease organisms may be introduced, to infect native species as well as the exotics; some introduced forms hybridize with the indigenous ones; through competition or predation, the native fishes and invertebrates may be depleted or even exterminated. Fishing in itself disturbs the balance of nature.

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[1] Contribution from the Scripps Institution Oceanography, New Series, No. 394.

Consistency would seem to demand the strict preservation of all the native aquatic life as well as all the native terrestrial life of the Parks, but such a policy could hardly be established now. Sport fishing has become a vested right of the Park visitors and is one of the outstanding recreational assets. Furthermore, legislation is involved. After considering this conflict in policy and practice, the Park Service has reached a realistic compromise policy, which calls for the preservation of the native aquatic life where it still exists, but which permits stocking of fish and allows fishing for sport where the natural balance has already been greatly disturbed (see statement of policy in the current edition of "Fishes of Yosemite National Park"). We urge a trend toward a more preservationist policy wherever this is practicable.

So far as the native fish life is concerned, there seems to be little fear that sport fishing will further greatly modify the natural conditions in Yosemite National Park. The native stock of rainbow trout has no doubt been modified by hybridization with introduced stocks, representing different races of the same species, or has been more or less completely replaced by the exotic races; the original characteristics of the local form of the Merced River can probably never be learned. The only other native species now of wide occurrence in the Park, the Sacramento sucker, is maintaining itself, despite the predation that must be exerted against it by trout. Such predation may be effected chiefly by the brown trout, which is usually more piscivorous than the other trouts. Except on the floor of Yosemite Valley, the rainbow trout is maintaining its abundance in competition with the brown trout. Even if all stocking of brown trout should be abandoned, this European species, which is particularly resistant to depletion, might continue to exist indefinitely in the Valley. The other native fishes, three minnows and one sculpin, appear to occur naturally in the Park only in the lower stretches of the Merced River. They may ascend to the power dam in the Merced Canyon but if so, they are blocked by this obstacle from reaching the seemingly more habitable waters of Yosemite Valley. They may originally have transgressed the turbulent waters of the Canyon at favorable times, to populate the relatively quiet waters of the Valley, but if so, they were prabably eliminated there by the brown trout or by the floods. Re-entry into the Valley would have been prevented by the dam.

More natural conditions for fish life in the Merced River and other Yosemite waters might be restored, but only by such measures as: (1) cessation of all further stocking of the exotic brown trout (in line with the present policy and program of the State Division of Fish and Game, which has restricted the propagation of this species, regarded as generally objectionable, almost entirely to National Park waters); (2) increased stocking of rainbow trout on the Valley floor, perhaps using larger fingerlings, or even yearlings or adults; (3) propagation of the rainbow trout of Yosemite Park waters or of other nearby Sierra Nevada waters, rather than those of distant regions, in order to maintain a stock as nearly like the original as would now be possible; (4) lessening or removal of fishing restrictions on the brown trout, or its depletion in the

Valley by other means; (5) protecting the rainbow trout, particularly in the Valley; (6) removal of the power dam, to permit the natural movement of rainbow trout and other native species from the Canyon into the Valley. These measures could be invoked in any combination. The first two to four would seem to be the least objectionable and the most practicable. We urge the consideration of these suggested measures by the Park authorities and recommend that the stocking of brown trout be stopped and that at least one of the other measures be adoped.

PREVIOUS REPORTS OF NATIVE FISHES

The first published notice of the fish life of Yosemite National Park that has come to our notice was a brief statement by J. M. Hutchings (1886, p. 363), one of the pioneer hotel managers. He wrote: "There are but two kinds of fish in this river [the Merced], or in any of its tributaries, speckled (rainbow) trout and [Sacramento] suckers."

In the second report cited above, Evermann (1921, p. 200) stated that "the fish fauna of Yosemite National Park is not a rich one," adding that "of native species there are two suckers, three minnows, and one trout; and of these only the trout is at all common." This general statement is true, but the species list as given was hypothetical and in part incorrect. When the report was written none of the putative native species other than the rainbow trout was known by Evermann to occur within Yosemite boundaries. He stated, "there remain but two suckers and three minnows that might be found within the park." Of the five kinds mentioned, one sucker, **Catostomus occidentalis**, and two minnows, **Mylopharodon conocephalus** and **Ptychocheilus grandis**, have since been taken in the Park. One of the others, **"Pantosteus araeopus,"** is currently treated as a synonym of **Catostomus occidentalis.** The fifth, **Siphateles formosus**, was either a lowland type, now probably extinct, or was incorrectly ascribed to the Merced River and to the Sacramento River system.

Bryant in 1929 (p. 143) definitely indicated that the sucker **(Catostomus occidentalis)** is an inhabitant of the Park and noted that the "Sacramento Pike or Squawfish" (referring to **Ptychocheilus grandis)** had "been taken in the Merced River close to the park line." He mentioned also: "Split tail. Native. Occasionally caught in Moss Creek near El Portal. Not known to have been taken within the park boundary." But the splittail is **Pogonichthys macrolepidotus** (Ayres), an inhabitant of the lower, main rivers in the Sacramento Valley. It probably never ascends to such high elevations. Since Bryant gave no scientific name for this species and since no specimens have been found to support the record, we have assumed that no authoritative identification was made. Word just received from him confirms this assumption. The record was based on the report of fishermen who had caught some fish, probably **Mylopharodon conocephalus** or **Ptychocheilus grandis** that they called "splittail."

In the fourth report on Yosemite fishes, Evans (1944, pp. 10-11; 1947 ed., pp. 8-9) listed, in addition to trout, one sucker, **Catostomus occi-**

dentalis, and two minnows, **Mylopharodon conocephalus** and **Hesperoleucus symmetricus.** All were recorded from within the Park, but the species last named was regarded as introduced.

NEW DATA ON THE NATIVE FISHES

We now add two species, both native, to the known fish fauna of Yosemite National Park, namely the Sacramento squawfish, **Ptychocheilus grandis**, and a sculpin, the riffle muddler, **Cottus bairdii gulosus.** We further show that the minnow **Hesperoleucus symmetricus**, previously thought to be introduced only, is really native in the Park. We thus add three species to the recognized native fish fauna of Yosemite National Park, doubling the list. The total fauna comprises the six species listed below: one trout, one sucker, three minnows and one sculpin. Of the six only the trout and the sucker are known to be of native occurrence in any of the Park waters, other than the Merced River in the Canyon, at the lowest elevations within the Park boundaries. Probably only the trout and the sucker are native to the Tuolumne River within the Park. The Tuolumne leaves the Park at a somewhat higher elevation (about 3,150 feet) than does the Merced (about 2,200 feet). These are the only rivers whose headwaters drain Yosemite National Park as at present delimited.

COMMON RAINBOW TROUT

Salmo gairdnerii irideus Gibbons

Despite all the attention that has been given the rainbow trout (including the steelhead), by ichthyologists, fishery biologists and fish-culturists, not to mention myriads of anglers, much doubt and confusion persists regarding the systematic status and scientific nomenclature of its several subspecies. There is rather general agreement only on the species name, **Salmo gairdnerii** (Richardson). Our tentative opinion is that the Yosemite trout of this species should be referred to **S. g. irideus**, which name we use for the wide-spread, generally nonmigratory, moderately coarse-scaled, relatively deep-bodied, big-headed and big-finned types. The Yosemite form has been referred to **"Salmo shasta,"** the Shasta rainbow trout of fish-culturists, but a recent examination at Stanford University of the type specimens of **Salmo gairdneri shasta** Jordan, by Hubbs and Follett, failed to disclose any valid reason for even the subspecific recognition of **shasta.**

It is possible that the Yosemite waters were originally populated by a slightly differentiated race of rainbow trout, but, as noted earlier (p. 132), it will probably never be possible to determine what were the characteristics of the indigenous stock or stocks. Here as elsewhere the local forms have been much contaminated and confused by the almost indiscriminate mixing indulged in by fish-culturists. Such interference with the natural order is especially to be decried in the National Parks, which are supposedly consecrated to the strict preservation of nature and of all native life within the park boundaries.

Rainbow trout were presumably native in Yosemite Park in most of the waters at moderate elevations, in both the Merced and Tuolumne river systems. The species is treated in the four reports on Yosemite fishes cited earlier, and in several angling books, notably that of McDermand (1941). Lee-mee, one of the surviving Indians of the Yosemite region, who has interpreted the life of the local aboriginies for the Park Service, states that trout occurred in Yosemite Valley prior to the occupation of the valley by white men, but that the Indians held them in lesser esteem than the suckers. Obviously this view was not shared by the early white settlers, for Hutchings (1886, p. 363) wrote that the "trout, you will find, are a delicious table fish; but no one except Indians, will think of eating suckers."

There is no reason to believe that rainbow trout or any other kind of fish ever occurred in any of the Park waters above the free-leaping waterfalls of Yosemite and Little Yosemite valleys. This view is verified by a letter written to Mr. Chester Verteeg on July 12, 1924, by Colonel H. C. Benson, one of the early Park Superintendents. Colonel Benson stated: "When we went into the Yosemite Park there were no fish in the Park except those which were enabled to come directly up the Merced River to the Yosemite Valley and up the south fork of the Merced to within a mile or two east of Wawona and up the Tuolumne to the falls of the Hetch Hetchy except the fish that were found in Lake Eleanor and its immediate tributaries which fish had been brought in by old man Kibbe in 1877. He had put fish in Lake Eleanor and Lake Vernon but they were unable to get back into the country behind the falls of Lake Eleanor."

Since the early years of Park history rainbow trout and other exotic species have been stocked in many of the higher waters. They have spread from points of stocking upstream as far as they could go. Downstream they may not have been stopped even by the high falls. Trout have been caught between the successive leaps of Yosemite Falls and there are no records of stocking that part of Yosemite Creek. Experiments by the senior author showed that small fish may be dropped until they attain the maximum velocity of fall, without harm if they land in water or even on hard wet surfaces.

Rainbows are caught more commonly in the Merced Canyon than in Yosemite Valley. They were seen in marked abundance in pools below the power dam. On the morning of July 31, 1948, 28 adults were counted in a single pool and on the upper part of the riffle below. There is some natural reproduction of rainbows.

The differential abundance of the rainbow and brown trout of Merced River in the Canyon and in the Valley apparently reflects the recent stocking practice as well as natural habitat selection. Alan C. Taft, Chief of the Bureau of Fish Conservation of the State Division of Fish and Game, which operates the fish hatchery in the Park, writes under date of October 19, 1948, that: "During the last few years we have planted the Merced River in the floor of Yosemite Valley with approximately 100,000 brown trout fingerlings each year. About the same number of rainbow have been planted but they have been largely concentrated in the swifter water between the power house and El Portal. Only the larger of our rainbow fingerlings have been planted in the floor of the Valley."

SACRAMENTO SUCKER

Catostomus occidentalis Ayres

This species, the common sucker of the Central Valley, probably occurs throughout the Merced and Tuolumne river systems from low elevations in the San Joaquin Valley to moderate elevations in Yosemite National Park. Hutchings (1886, p. 363), wrote of its occurrence, habits and utilization by the Indians in Yosemite Valley. As noted above, one of the surviving Indians of the Valley states that his people preferred suckers to trout. Rutter (1908, p. 124) reported it from the Merced at Benton Mill and Livingston, from the Tuolumne at Baker Ford and from the South Fork of the Tuolumne near the mouth. It was found to be common in the Merced at Indian Flats (1,550 feet elevation) by Taft, Shapovalov, Needham and Sumner in July, 1933, and by Hubbs and Miller on July 24, 1938. Evermann (1921, p. 200) indicated that it might be found within Yosemite Park. Bryant (1929, p. 143) reported it as native in the larger streams, adding that it had supposedly been introduced into Tenaya Lake. Evans (1944, p. 10; 1947 ed., p. 8) wrote that it is common in the Merced and Tuolumne rivers at the lower elevations within the Park, but that it is seldom at home above the lower valley levels. In the summer of 1948 we found the species common in the quieter pools and margins of the Merced River from the west boundary (about 2,200 feet) through the Canyon and Valley at least to Mirror Lake (about 4100 feet). None were seen by us in Tenaya Lake (8,141 feet), but our observations there were brief and we heard several reports of the occurrence of suckers and also of "chubs." Leo Shapovalov tells us that large suckers were found by the 1933 survey to be common in Tenaya Lake. Because of its high elevation, it is extremely improbable that such species are native to this lake.

Adult and half-grown suckers are more or less solitary inhabitants of the deeper, quieter pools of the Merced River. They may be seen from early morning until night, leisurely mouthing their way over the rock surfaces in search of food. Using their very fleshy papillose lips, they work like a vacuum cleaner.

The very young, in contrast, swim in loose to dense schools at various water levels, near the quiet margins and in small side channels. On July 31, 1948, such young-of-the-year abounded at the margins of the Merced River near the west boundary of the Park and at various points between there and the Valley. They were still very small and extremely slender (such fry can be recognized as suckers by their slenderness and by the extension of the intestine to near the caudal fin). A sample of 82 specimens dip-netted from several of the small schools ranged in standard length from 12 to 21 mm. and averaged 15.0 mm. (slightly more than one-half inch). Until disturbed most of the fry swam near the surface, but the largest ones were beginning to live on the bottom, forsaking their early plankton-feeding habits.

Growth of suckers in the Merced River must be very slow, for 54 yearlings seined on July 31 (50 about one-half mile below Cascade Creek and 4 in the Valley) ranged in standard length from 33 to 64 mm., with an average of only 47.3 mm. (less than 2 inches). Large numbers of yearlings of this size range were observed in the quieter side channels and on quiet sandy shallows. Like the adults, they were feeding on the bottom. The first winter annulus is close to the center of the scales and is indistinct. One two-year-old sucker in the July 31 collection, 107 mm. (slightly over 4 inches) in standard length, has a definite winter annulus near the margin of each scale.

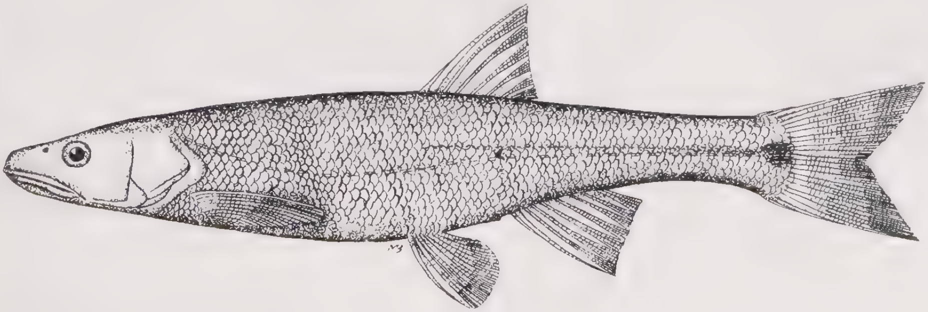
The very slow growth of suckers in Merced River is attributable to the purity of the snow-fed water and to the scouring of the bottom by high water in the spring. By the end of July (when our collection was made) young-of-the-year suckers in a Michigan lake are as large as the yearlings in Merced River (Hubbs and Creaser, 1924). Growth is also much less rapid than in a lake in northern Wisconsin (Spoor, 1938), but more in accord with that reported by Stewart (1926) for certain streams in New York. The eastern suckers are referred to a different though very similar species, **Catostomus c. commersonnii.**

SACRAMENTO SQUAWFISH

Ptychocheilus grandis (Ayres)

Published reports have indicated the occurrence of this species in the Merced River, but only at elevations lower than the western boundary of Yosemite National Park (about 2,200 feet). It is wide-spread in the Central Valley of California (Evermann and Clark, 1931, pp. 52-53). Rutter (1908, p. 133) listed it from the Merced at Livingston and Benton Mill. Evermann (1921, p. 200) wrote that it might occur within the Park and Bryant (1929, p. 141) indicated that it had been taken in the Merced close to the Park line.

Anglers have reported for several years the capture of "pike"—a common misnomer for this very large and voracious minnow—about El Portal and in pools in the Merced Canyon above the Park boundary. On July 31, 1948, we verified these claims by finding right at the boundary a half-grown specimen 230 mm. in standard length; obviously it had been caught in the river and had been thrown out by a disappointed trout angler. Later we learned that a specimen had been taken in the Park by the fish survey of 1933, con-



Sacramento squawfish, *Ptychocheilus grandis*, drawn by Ranger Naturaliist Martin R. Brittan from a 6½-inch specimen from Merced River.

ducted by Taft, Shapovalov, Needham and Sumner. It was caught on August 18 in the Merced River 1.5 miles above El Portal and 0.2 mile within the Park boundary. No evidence was obtained to indicate that this species occurs above the power dam in the Merced Canyon and it must be rare between the dam and the boundary.

The fact that the specimen taken in 1933 was a yearling suggests that the species spawns within the Park, for the river in the Canyon is apparently too swift to be ascended by small minnows. It reproduces freely in the Merced River at Indian Flats, at an elevation of about 1,550 feet. Numerous young to half-grown specimens were taken there during the 1933 survey and yearlings were seined at the same place by Hubbs and Miller on July 24, 1938.

This large-mouthed minnow reaches a length of over three feet and is reputed to be very destructive to trout and salmon. Its predatory habits, however, should not be taken as an excuse for its destruction within the Park. Since it is of such rare though natural occurrence, it should be protected by the Park regulations.

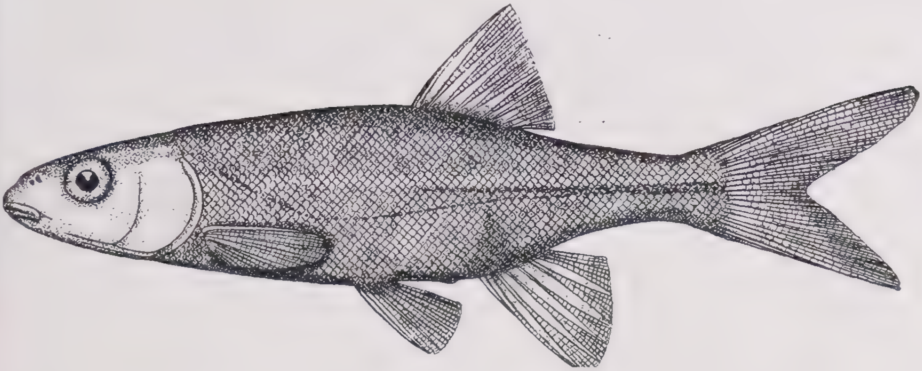
HARDHEAD

Mylopharodon conocephalus (Baird and Girard)

The inclusion of this large minnow in the Yosemite National Park list rests on the statement by Evermann (1921, p. 200) that it might occur and on the definite record by Evans (1944, p. 10; 1947 ed., p. 8), of a specimen collected on July 26, 1934, in the Merced River one-half mile below Arch Rock Entrance Station, at an elevation of about 2,800 feet. It was caught by Mrs. F. M. Watson and was received and accessioned by A. E. Borell. The identification was confirmed on July 31, 1948, by a re-examination of the specimen in the Yosemite Museum (No. 139).

This species is somewhat smaller than the squawfish, seldom reaching the length of two feet. It has a smaller mouth and a less slender head. It differs sharply in having the upper lip nonprotractile (bound to the forehead by a bridge of skin, the frenum) and in having a much shorter bony pharyngeal arch (in the throat), with molar rather than slender, hooked teeth. These differences in structure indicate that the hardhead is much less predacious than the squawfish. (Follett, 1928.)

The hardhead is probably uncommon within the Park and is almost certainly confined there to the lower elevations of the Merced Canyon. The few that ascend the stream beyond the Park boundary (at about 2,200 feet) are perhaps strays from Indian Flats (about 1,550 feet), where many young and yearling specimens and some older ones were taken during the survey of July-August, 1933. At the same place Hubbs and Miller took yearlings on July 24, 1938. Rutter (1908, p. 129) got specimens farther down the Merced River, at Livingston and Benton Mill. The species is widely spread through the Central Valley (Evermann and Clark, 1931, p. 52), particularly in the foothill region.



Chub-roach, *Hesperoleucus symmetricus*, drawn by Ranger Naturalist Martin R. Brittan from a 3½ inch specimen collected by Rutter in Merced River at Livingston.

SIERRA CHUB-ROACH

Hesperoleucus symmetricus (Baird and Girard), subspecies

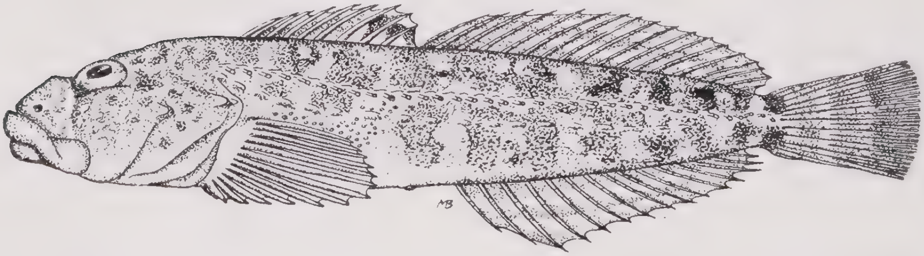
This somewhat speckled, finger-length minnow was reported from Yosemite National Park by Evans (1944, pp. 10-11; 1947 ed., pp. 8-9). In the Park it has been known only in Hetch Hetchy Reservoir and it is said to have first appeared there in 1930. Apparently on circumstantial evidence it has been assumed that it was introduced by the dumping of live bait. That may well be true, but it is also wholly possible that it existed in small numbers in the Tuolumne River in Hetch Hetchy Valley (elevation 3,680 feet), prior to the impoundment, and that it did not build up a conspicuous population in the lake until 1930. The possibility that the species naturally ascended the Tuolumne to populate Hetch Hetchy Valley finds support in our discovery of its occurrence and breeding in the Merced River at the western boundary of Yosemite National Park, at an elevation of about 2,200 feet.

The discovery of this minnow in the Merced River at the park boundary came about in an unexpected way. It was not recognized during the examination on the river on July 31, 1948. On sorting the collection of fry dip-netted on that day in the quiet margins of the river, it was noticed that the six smallest specimens, each 9 mm. (⅜ inch) in standard length, were minnows, not suckers. The expectation that these lavae might represent **Hesperoleucus symmetricus** was verified by comparing the specimens with Fry's (1936) excellent figures and descriptions of the developmental stages of the Baystream chub-roach, **H. s. venustus** Snyder. In all details of form and proportions, position and development of fins, and pigmentation, our 9 mm. postlarvae are just intermediate between the 8.5 and 9.5 mm. stages figured by Fry. There seems to be no doubt about the specific identification.

In all probability **Hesperoleucus symmetricus** is native in the Merced River within the Park, though it is undoubtedly scarce at elevations above 2,000 feet. It is probably very inconspicuous there, for in the swift water it would tend to seek retreat under boulders. Those that do occur so far upstream (and at least occasionally breed there) presumably stem from a rather large population in the river at Indian Flats (about 1,550 feet). Many young to adult specimens were taken there during the 1933 survey and yearlings plus two adults were seined at the same place by Hubbs and Miller on July 24, 1938.

The species **Hesperoleucus symmetricus** is of wide occurrence through the Central Valley of California and in the contiguous coastal streams (Snyder, 1913, pp. 63-70). In the Merced and Tuolumne river systems it is probably common at many places below the localities already mentioned. Rutter (1908, p. 139) had it from the Merced at Benton Mill and Livingston, from the North Fork of the Merced at Bower Cave, from the Tuolumne at Baker Ford, and from the South Fork of the Tuolumne near its mouth.

The subspecies that occurs in and near Yosemite National Park appears to be one of the several local forms that are still unnamed. Snyder named a number (giving them full species rank), but, overimpressed with the importance of geographical segregation in separate stream systems, he did not distinguish subspecies within the Sacramento-San Joaquin system. Rutter (1908, pp. 137-139) had already pointed out marked local variations, even within the Merced River system. Much of the differentiation appears to be ecotypic. The typical subspecies, **H. s. symmetricus**, inhabiting the main rivers with a strong and constant current, has a very slender caudal peduncle and long, expansive and falcate fins, the dorsal usually with 10 and the anal ordinarily with 9 rays. The unnamed foothill form, inhabiting the quieter spots of the smaller pool-and-riffle streams, has a chunkier build with deeper caudal peduncle and smaller, more rounded fins, the dorsal usually with 9 and the anal ordinarily with 8 rays. These contrasting but intergrading types are paralleled by ecotypic subspecies in many species of western fresh-water fishes (Hubbs, 1940a, pp. 199-200; 1941, pp. 186-187). The character gradients are repeated again and again in close correlation with the biological gradients.



Riffle muddler, *Cottus bairdii gulosus*, drawn by Ranger Naturalist Martin R. Brittan from a 5-inch specimen from Merced River in Yosemite National Park.

RIFFLE MUDDLER

Cottus bairdii gulosus (Girard)

This fresh-water sculpin is another addition to the known fish fauna of Yosemite National Park. It was reported by Rutter (1908, p. 146) southward only to Stanislaus River, the first main stream north of the Tuolumne. Dill (1946, pp. 54-55) reported a species of **Cottus** from the San Joaquin River, the first main mountain stream of the Merced, but a specimen from Millerton Lake, submitted by him, proves to be **Cottus asper** Richardson. We find no published records of any **Cottus** for either the Tuolumne or the Merced system. The occurrence of the species in Merced River is substantiated by four collections, each of a single specimen and all from within the Park. The first three specimens are in the Yosemite Museum, the fourth, in the University of Michigan Museum of Zoology. The data follow:

One adult from Merced River below the dam and above Arch Rock Entrance Station, at an elevation of about 3,700 feet; caught by Mrs. Lucy Cleveland on July 14, 1934, and received by A. E. Borell.

One adult from Merced River near the Incline; caught by a woman angler on July 10, 1938.

One adult from Merced River at Steamboat Bay (a large stream pool), at an elevation of about 3,600 feet; caught on a worm by Erwin Brocker on August 22, 1938.

One half-grown specimen 52 mm. in standard length, from the Merced River at the west boundary of the Park (about 2,200 feet); taken by us in a small seine by overturning boulders, on July 31, 1948.

The species must be rare in the Merced River. The lower courses of the river in San Joaquin Valley do not provide suitable habitats. No specimens were found among the many fishes collected during the 1933 survey, either at Indian Flats (about 1,550 feet) or in the Park. None was obtained at Indian Flats by Hubbs and Miller on July 24, 1938, though special effort was made to collect sculpins by methods that are usually productive—overturning boulders and stones and kicking in vegetation, in such a way that the fish are swept into a small seine set below and partly around the operation. Such methods employed on July 31, 1948, yielded only the one specimen at the park boundary and none in the river below Cascade Creek or on the Valley floor.

According to L. C. Nixon, foreman of the local State fish hatchery, the "bullheads" that occur in Merced River near the western Park boundary reach a length of six inches.

The muddlers or fresh-water sculpins (miller's thumb and bullhead are other names) are small scaleless (sometimes prickly) fishes with expanded pectoral fins, the pelvic (ventral) fin below the pectoral base, two dorsal fins (the first with low, threadlike spines), a broad and rather flat head, a small eye on the upper part of the head, one or more small preopercular spines (on the side of the head), and rather dark, usually mottled color.

The systematics of the American species of **Cottus** is in a state of uncertainty. The far-western form that has generally been named **C. gulosus** should apparently be treated as a subspecies of **Cottus bairdii**, for **gulosus** and **C. b. bairdii** (of eastern North America) seem to belong to the same wide-spread and variable species complex. The form **gulosus** as currently recognized is perhaps in itself a complex of subspecies and it is not certain that the Merced River form should be identified as **C. b. gulosus.** Several of the local forms in the Sacramento system, including the one named **Cottus shasta,** seem to be worthy of subspecific separation.

In view of the confusion that exists, we give some of the salient features of the four specimens from the Merced River. The lateral line is complete. Palatine teeth are well developed. Prickles are confined to the axil. The dorsal fins are only slightly connected. The fin rays number: dorsal spines, 9; dorsal softrays, 18 (in 3) or 19 (1); anal rays, 13 (1) or 14 (3); pectoral rays, 15 (6 fins) or 16 (2 fins); pelvic rays I, 4; principal caudal rays, 10 (1) or 11 (2).

OTHER SPECIES OF POSSIBLE NATIVE OCCURRENCE

It seems doubtful to us that there will be any further increases in the list of fishes known to be native in the waters of Yosemite National Park. Even a considerable extension of the boundaries (or a considerable trip beyond the present limits) would probably add none. The Mono Lake drainage basin across the Sierra rim to the eastward seems to be devoid of native fish life (Hubbs and Miller, 1948, pp. 78-79). It is unlikely that the Park area will be extended far enough to the northeastward to include waters in the Walker River system that contain native Lahontan species. An extension of the boundary in the mountains northward or southeastward or southward would presumably bring in no additional species. An extension to much lower elevations to the westward would probably be required to add other species.

There are now known from within the Park all species that have been obtained during extensive collecting in the Merced River at Indian Flats at an elevation of about 1,550 feet. Collections were made there in July and August, 1933, during the fish survey conducted by Alan C. Taft, Leo Shapovalov, Paul R. Needham and Francis H. Sumner, and on July 24, 1938, by Carl L. Hubbs and Robert R. Miller. Both parties collected only **Catostomus occidentalis, Ptychocheilus grandis, Mylopharodon conocephalus** and **Hesperoleucus symmetricus.** We are greatly indebted to Mr. Shapovalov, now with the California State Division of Fish and Game, for permission to examine and to list fishes taken during the 1933 survey.

Since none of the other, more lowland species of the Central Valley were obtained at 1,550 feet in Indian Flats, it is extremely doubtful that any of them have ever reached the Park boundaries, or will likely do so by natural dispersal. Exclusive of the anadromous forms which with even greater assurance can be regarded as unable to reach the Park at present, these lowland forms may be listed as follows:

Lampreys, family Petromyzonidae: European brook lamprey, **Lampetra planeri** (Bloch).

Minnows, family Cyprinidae: blackchub, **Orthodon microlepidotus** (Ayres); splittail, **Pogonichthys macrolepidotus** (Ayres); thicktail, **Gila crassicauda** (Baird and Girard); Sacramento hitch, **Lavinia e. exilicauda** Baird and Girard; Sacramento tui, **Siphateles obesus formosus** (Girard).

Sunfishes, family Centrarchidae: Sacramento-perch, **Archoplites interruptus** (Girard).

Surfperches and seaperches, family Embiotocidae: valleyperch, **Hysterocarpus traskii** Gibbons.

One other minnow species listed by Rutter (1908, pp. 139-140) as **Agosia robusta** but now called **Rhinichthys osculus,** occurs at various elevations in the Sacramento-San Joaquin system, but oddly seems to skip the Yosemite region in its distribution. The subspecies of this river system are undetermined.

The fish fauna of Yosemite National Park is limited and restricted by the steep gradient of the streams and by the torrential rush of water during the rapid melting of the deep snowfall on the Sierra Nevada. Many species of the Sacramento fauna fail to ascend either the Merced or the Tuolumne River to the western boundary of the Park (at elevations of about 2,200 and 3,150 feet, respectively). Four of the six kinds that are known to have extended their range beyond the boundary appear to be confined to the lower elevations of the Merced River Canyon. It is possible that they originally occurred as high as Yosemite Valley (3,900 to 4,100 feet elevation), but, if so, they have probably been extirpated there by high water, by the power dam that prevents reinvasion and by the predation of trout, particularly brown trout. Among the native fishes only the rainbow trout and the Sacrameno sucker are definitely known to occur either in Yosemite Valley or in the Tuolumne River system within the Park boundaries. Suckers and trout are particularly adept in surmounting torrential waters. As would be expected, no native fish occur above the high plunging falls of Yosemite National Park.

SUMMARY AND CONCLUSIONS

The National Parks have been consecrated to the strict protection of that part of the native animal and plant life which lives above the water surface, but the Park Service has commonly treated the aquatic life as a recreational asset. Hunting is prohibited but fishing is often encouraged. Exotic terrestrial animals are rigidly excluded but exotic fishes have often been stocked. A compromise policy has been adopted. It calls for the preservation of aquatic life in the Parks where conditions are yet unspoiled and otherwise to some degree restricts the recreational developments. The trend toward a preservationist policy for the aquatic life might well be extended when and where it would be practicable to do so. In Yosemite National Park, however, fishing under present regulations will probably have relatively little further effect on the native aquatic life. Drastic measures would be needed to improve very markedly the natural biotic conditions in the streams. It is recommended, however, that the stocking of the exotic brown be discontinued.

Hitherto only three fish species have been reported as native in Yosemite waters—rainbow trout, **Salmo gairdnerii irideus;** Sacramento sucker, **Catostomus occidentalis;** and a large minnow, the hardhead, **Mylopharodon conocephalus.** We now double the list, adding two minnows (the squawfish, **Ptychocheilus grandis,** and a chub-roach, **Hesperoleucus symmetricus)** and also one fresh-water sculpin, the riffle muddler, **Cottus bairdii gulosus.** Notes are included on the biology of the six native species, including a brief study of the slow growth of the sucker. It is unlikely that any additional native species will be discovered in the Park waters.

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Contribution No. 395

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NECROLOGY

WINFRED EMORY ALLEN
1873–1947

Winfred Emory Allen, Assistant Professor of Biology Emeritus of the Scripps Institution of Oceanography of the University of California died after a short illness on Sept. 20, 1947. While he had wide interests in biology reflected in his numerous published notes of significant observations in natural history, he was best known for his extensive studies of the abundance of marine phytoplankton particularly in the eastern North Pacific.

Besides graduating from Earlham College in 1898 and obtaining his master's degree at Lawrence College in 1904, Allen worked and taught at the universities of Nebraska and Illinois with Professor Henry B. Ward. His interest in athletics shown by his activities as coach and director of physical education at these institutions remained with him all his life. For several years he taught biology in high schools on the Pacific Coast and while head of the department of biology at the Stockton California High School collected the data for his first major work on the plankton of the San Joaquin River (1920).

In 1919 began his connection with the Scripps Institution for Biological Research (now the Scripps Institution of Oceanography) which lasted until 1946, only a year before his death. During this period he devoted his attention almost exclusively to quantitative studies of the marine phytoplankton, particularly of the waters off southern California. In connection with oceanographic cruises at various times in adjacent areas he also obtained series of collections and made similar studies of the abundance of phytoplankton in the eastern North Pacific from Alaska to Ecuador and as far out to sea as Hawaii. He early devised standard collection methods involving filtering or settling of the contents of water samples and invented a closing bottle which bears his name. He also determined the minimum size of sample in which organisms could be enumerated with satisfactory accuracy. He inaugurated the daily collection of samples at two points on the California coast which has been continued for over twenty-five years and studied the samples collected. The results of the latter operations have been largely embodied in two reports on quantitative studies of plankton diatoms and dinoflagellates during a twenty year series. With H. U. Sverdrup and J. Y. Gilbert he published papers relating the abundance of phytoplankton off southern California and in the Gulf of California to the hydrographic conditions in those areas. As a result of his single-hearted devotion to the subject, the Scripps Institution has a record of the numerical abundance of phytoplankton in the local waters which is unparalleled for continuity in both space and time.

Allen was a member of the Ecological Society of America, the American Microscopical Society, the Limnological Society of America, the Western Society of Naturalists and the Botanical Society of America. He was widely known and respected on the Pacific Coast for his range of information on the natural history of marine organisms and his independent point of view on many subjects related to marine life.

MARSTON C. SARGENT
Scripps Institution of Oceanography

Contribution No. 397

Transactions, American Geophysical Union Volume 29, Number 4 August 1948

RESEARCH WITHIN PHYSICAL OCEANOGRAPHY AND SUBMARINE GEOLOGY AT THE SCRIPPS INSTITUTION OF OCEANOGRAPHY DURING APRIL 1947 TO APRIL 1948

G. F. McEwen and Staff

Emphasis is placed on the activities within the fields of submarine geology and physical and chemical oceanography, although extensive researches within the biological fields are carried on at the Scripps Institution of Oceanography.

Tracking storms by forerunners of swell--Walter Munk has worked out relationships for computing the travel time and distance of a storm from the characteristics of swell observed at the shore station. The paths for storms computed from wave records compare favorably to those shown on the weather maps.

Wave action on structures--Munk has developed equations for estimating the forces and moments exerted by waves on vertical cylindrical beams.

Critical wind speed for air-sea boundary processes--Munk has summarized observations of rapid changes in the character of certain boundary processes at a wind speed of about 6.5 m/sec. These abrupt changes are related to the hydrodynamic character of the sea surface which has been described by Rossby and Montgomery. The change in character of the sea surface is also related to the Kelvin-Helmholz criterion for the instability of small waves in the presence of a shear.

Dynamic aspects of the equatorial current changes--Sverdrup and Reid have re-examined the dynamic aspects of the Equatorial Current changes. In the eastern Pacific they found that observed conditions can be accounted for by an application of the equations of motion involving the following forces: pressure gradients, Coriolis force, and wind stress applied at the sea surface.

Variability in direction of wave travel--R. S. Arthur has computed the growth of waves moving at an angle with the wind by generalizing the wave forecasting relationships of Sverdrup and Munk. Results agree with forecasting experience, and with observations made off San Clemente Island and the Island of Sicily.

Hawaiian swell from January 2-5, 1947--Unusually high swell from a storm 500 mi north of the islands caused damage estimated at $2,000,000 during this period. Although the waves were described as the highest in 45 years, the study by Arthur shows that existing forecasting methods giv accurate values of wave height at least 24 hr in advance of occurrence. The situation affords an unusual opportunity for checking a revised travel-time relationship.

Revised wave-forecasting graphs and procedure--Arthur has completed the preparation of forecasting graphs based on the revised forecasting theory given by Sverdrup and Munk in Wind, Sea, and Swell, H. O. Pub. No. 601. Procedures have been revised on the basis of recent experience and research.

Diffraction of water waves by breakwaters--J. A. Putnam, of the Department of Mechanical Engineering, University of California, Berkeley, and R. S. Arthur have made application of a solution of the water wave-diffraction problem of Penney and Price to diffraction by a semi-infinite impermeable breakwater. Results from tank experiments verify the general form of wave-diffraction theory.

Sea surface-temperature variations influencing fog formation in Southern California--D. F. Leipper has discussed the relative importance of factors and processes affecting sea-surface temperature. Suggestions are made for predicting short period changes in the pattern of sea-surface isotherms with particular emphasis being given to the necessity for considering the initial temperature-depth structure. Evidence is presented to show that the sea-surface temperature is an important factor in fog formation in the San Diego region.

orecasting coastal fog--Leipper has defined three non-diurnal indices in such a manner that l not form in the San Diego area unless these indices fall within certain critical ranges. The s are related to the physical processes by which fog forms. They have been checked statis- over a three-year period and only one brief fog occurrence was found with the indices out- e critical range. The indices are height of the inversion base, which must be less than 1300 fog to form; the temperature difference between the sea surface and the air at the altitude maximum temperature on the morning radiosonde, where the air temperature must be the ; and the temperature difference between the sea-surface temperature and the afternoon e dew point, where the dew point must not be more than 9°F below the sea temperature if to form within 24 hr.

rea studies--Leipper, in conjunction with W. W. Wood, has prepared a report entitled erature and Salinity of Philippine Waters. He has carried out a preliminary study Sea erature in the Hawaiian Island Area which is being enlarged and completed by E. R. Anderson.

e has made an Analysis of Bathythermograms for Operation Highjump. This analysis was with Luis Capurro, Lt., Argentine Navy, and Estil Hamill, Capt., AAF Weather Service, and es heat budget and temperature-distribution studies, a note on internal waves in the Antarctic, summary of processes affecting the melting point of sea water.

everal thousand sea-temperature measurements made by the bucket method in shallow water California beaches were studied to determine the diurnal variation and the relation to off- temperatures of these surf-zone values.

tudies of sea and swell--Two statistical studies of sea and swell conditions were made by E. derson, W. V. Burt, W. C. Thompson, and J. F. T. Saur, Jr., using weather data and the wave- asting procedure. A Statistical Study of Wave Conditions at Four Sheltered Areas was pre- for the United States Navy and A Statistical Study of Wave Conditions at Five Open Sea ities along the California Coast was prepared for the United States Engineer Office, Los es.

e method of using the wave-forecasting procedure and past weather charts to obtain sta- wave data has been described by Wayne V. Burt and J. F. T. Saur, Jr., in an article to be shed in an engineering journal.

alysis of ships' surface-current observations--The development and use of certain statistical eters obtainable from ships' surface-current observations were investigated by J. C. Arm- and W. W. Wood in an attempt to devise a more rational method of using ships' observations rents in the preparation of current charts. The use of probablility ellipses to indicate the ansport of water in a given region and the pattern of the fluctuations of the net transport was sed and a model current chart covering the area 0°-20°N, 115°-130°E was prepared using ethod. The final report prepared by D. W. Pritchard due to the departure of the original s is as yet unpublished pending comment by Armstrong.

bjective approach to the construction of streamlines of current flow--A system for the ob- construction of streamlines was considered by D. W. Pritchard, so that for a given current ution, as defined by the average current vectors, only one set of streamlines would be de- Because the vertical velocity field can be considered negligible, the horizontal velocity vas considered non-divergent and the stream function was applicable. By proper choice of the nts of integration two sets of linear stream function fields obtained by numerical integration North and South velocity components become equal and the complete stream function field ined. The method was tested for two areas and the results were encouraging.

Wind stress-analysis of the North Pacific--Saur has carried on a large amount of statistical in the Current Section to determine the resultant average wind-stress field in the North fic Ocean, and a similar project is being started for the North Atlantic Ocean. The procedure ves computing the resultant stress for each five-degree quadrangle from the wind roses ted on the Pilot Charts of the given ocean.

Theory of wind driven currents--Saur has carried on further investigations of the effects of rent wind-stress distributions and boundaries upon currents. This is based upon recent work . U. Sverdrup, indicating the close relation between the stress field and permanent ocean ents.

Daily temperature and salinity observations of the sea surface--Daily observations of sea-surface temperature and daily collected water samples have been obtained from five localities on the California Coast, exclusive of those taken at the Scripps Institution pier. The salinities of the samples have been determined by the specific gravity method. Other observations of surface temperatures have been obtained from the United States Lighthouse Tenders Sequoia and Lupine, and from tuna boats. The cooperation of organizations and personnel is greatly appreciated.

Oceanographic observations on the E. W. Scripps Cruises of 1941--The detailed results of these cruises, prepared by H. U. Sverdrup and the Staff of the Scripps Institution of Oceanograph have been published in a 160-page report.

Large horizontal eddies in the upper fifty meter ocean layer off Southern California--Result of investigations by G. F. McEwen of large counter-clockwise eddies so prevalent between a nort ward inshore current and a southward offshore current in this region are being prepared for pub lication. Convincing evidence from the formulation and solution of dynamical problems suggeste by these eddies supports the thesis that an observed series of eddies during a period of several months is a succession of stages of the expansion and decrease in velocity of the initial intense and relatively small eddy.

Investigations in submarine geology--These investigations under the direction of F. P. Shepa have included: (1) Longshore currents and their relation to wave trains and submarine topograph (2) observations with a new multi-sock sediment trap; (3) direct observations and photographing a diver, Frank Haymaker, of the precipitous and even overhanging canyon walls; (4) soundings showing the intricate gully pattern at the head of several of the canyons in the Southern Californi area; and (5) a survey along the Hawaiian coasts revealing the definite existence of submarine canyons off the deeply eroded Pali Coast of Oahu and Molokai.

Investigations in chemical oceanography--Work under the direction of N. W. Rakestraw included the design and construction of instruments for chemical work at sea, the study of oxygen consumption in sea water over long periods, and the study of arsenic in sea water, and the tolerance of marine organisms of it. Further extension of studies on the decomposition of organic matter in the sea is in progress.

Investigations of marine plankton--These investigations, under the direction of Martin W. Johnson, may be listed as follows: (1) Study of the deep scattering layer as related to plankton a other pelagic animals that undergo diurnal vertical migrations; (2) studies of the distribution an production of zooplankton in the offshore waters; (3) seasonal fluctuations and life histories of inshore plankton animals; and (4) further analyses of plankton observations made during Operati Crossroads.

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Dicyema paradoxum von Kölliker, 1849

The Mesozoa comprise one of the most controversial groups in the animal kingdom. The disagreement concerns their structure, life history, method of reproduction, and zoological status. The confusion arising from different interpretations of morphology and development is augmented by errors in nomenclature. Certain of these errors were rectified by Stunkard (*Amer. Mus. Nov.*, 1937, No. 908). Recently, study of the parasites of octopuses has necessitated a review of the literature on members of the family Dicyemidae.

The generic name *Dicyema* was selected by von Kölliker (*Ber. zoot. Anst. Würzburg,* 1849, 2, 59–66), since he first noted that these animals produce two distinct types of embryos, which he designated as ''wurmförmig'' and ''infusorienartig.'' The two kinds of embryos had been observed and described by Erdl (*Arch. Naturg.*, 1843, 9, 162–167), who regarded them as developmental stages of a single individual. Kölliker studied the parasites found in *Octopus vulgaris* and *Octopus macropus* and identified all the dicyemids found by him and those described by previous authors from other cephalopods as members of a single species, for which he proposed the name *Dicyema paradoxum.* The genus, as erected, was monotypic and *D. paradoxum* is the type species. The observations and descriptions of von Kölliker appear remarkably accurate and complete when compared with zoological reports of a century ago.

Subsequent investigations, however, have shown that *D. paradoxum* of Kölliker was a complex of several species. Van Beneden (*Bull. Acad. Roy. Belg.*, 1876, 41, 1160–1205; 42, 35–97) restricted the genus *Dicyema* to parasites of octopuses; those from *O. vulgaris* were designated as *D. typus* and those from *O. macropus* as *D. clausianum.* The name *D. paradoxum* was omitted. Holding a view diametrically opposed to that of von Kölliker, van Beneden believed in absolute taxonomic correlation between hosts and parasites. New genera were erected for the dicyemid parasites of each genus of cephalopods other than *Octopus*, and the parasites of the several cephalopod species were regarded as distinct. In van Beneden's system the family Dicyemide consisted of 4 genera and 7 species. Species described by Wagener (*Arch. Anat. Physiol. wiss. Med.*, 1857, 344–364) were redescribed and renamed when assigned to the new genera. Whitman (*Mitt. zool. Stat. Neapel*, 1882, **4**, 1–89) described additional new species and showed that van Beneden's idea of strict host-parasite specificity was erroneous; that the same species could infect more than one host species and that a single host could harbor more than one species of parasite. Whitman was meticulous in restoring names proposed by Wagener for species that had been renamed by van Beneden. He stated (p. 4): "... in systematic zoology the claims of priority are not to be superseded by those founded on accuracy of description." But van Beneden had also renamed the parasites described by von Kölliker as *D. paradoxum*, recognizing two species which he designated as *D. typus* and *D. clausianum*, respectively. Whitman accepted these names, and they have been adopted by subsequent authors. Nouvel (*Arch. Biol.*, 1947, **58**, 59–220) stated: "Pour Kölliker, le genre *Dicyema* comprenait tous les Dicyémides connus (*D. paradoxum*). Quand Whitman a créé un second genre (*Dicyemennea*), l'auteur a conservé, pour l'un des genres, le nom de *Dicyema* car le description de Kölliker est précisément fondée sur deux espèces qui restaient dans le genre ainsi restreint." It is clear, therefore, that the name *D. paradoxum* must apply to one of the two species now known as *D. typus* and *D. clausianum*. In an earlier paper, Nouvel (*Bull. Soc. Hist. Nat. Toulouse*, 1946, **81**, 169–174) redescribed *D. typus* as the smaller of the two species, with a smaller number of somatic cells (16–20), usually 18 or 19, and stated that in this species the diapolar cells never form pendant verruciform enlargements. According to Nouvel, *D. typus* occurs only in *Octopus vulgaris*, whereas *D. clausianum* occurs in both *O. vulgaris* and *O. macropus*. Moreover, Nouvel stated that earlier authors including van Beneden (1876), Whitman (1882), Hartmann (1906), Lameere (1914, 1916, 1918, 1919), and he himself in former papers, had identified individuals of *D. clausianum* as *D. typus.*

The International Code of Zoological Nomenclature provides that, if a species is divided into two or more restricted species, its valid name must be retained for one of the restricted species. Van Beneden (1876) did not admittedly divide the species *D. paradoxum*; instead, he redescribed the organisms as members of two distinct and restricted species for which he proposed new names, although both species were retained in the genus *Dicyema.* Indeed, they were the only species included in the genus. The procedure is clearly invalid, since the genus *Dicyema* is based on its type species *D. paradoxum.* Whitman and subsequent authors have perpetuated the error in accepting the two specific names proposed by van Beneden. Despite any disavowal, van Beneden virtually divided the species, and the name *D. paradoxum* must be retained for one of the restricted species which stands as type of the genus. As noted, either *D. typus* or *D. clausianum* must be relegated to synonymy. Since von Kölliker described and figured large individuals with prominent verruciform enlargements of the diapolar cells, it seems probable that his description applies more properly to the species called *D. clausianum* by van Beneden. Accordingly, *D. clausianum* van Beneden, 1876 is suppressed as a synonym of *D. paradoxum* von Kölliker, 1849.

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THE LIFE HISTORY AND BIOLOGY OF A MARINE HARPACTICOID COPEPOD, TISBE FURCATA (BAIRD) [1]

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Introduction

Only a few free-living marine copepods have been reared with a view to determining the details of their complete life histories. This can no doubt be attributed to the difficulty experienced in culturing most species through the entire life cycle. Considerable literature has accumulated on the morphology of developmental stages and on certain aspects of the biology, particularly of the more important planktonic calanoid species, especially *Calanus finmarchicus.* This species has also been reared through its entire life cycle in cultures (Lebour, 1916), and its biology studied under laboratory conditions more recently by Raymont and Gross (1942). The cyclopoid, *Oithonina nana,* has also been reared through the developmental stages (Murphy, 1923). But pertinent questions relative to the age at maturity, fecundity, and life span of individuals have received scant attention for other marine species. The fresh-water copepods on the other hand have been the subject of a large amount of investigation and much detail is known about their life histories and reproduction (see especially Gurney, 1931; Ewers, 1930, 1936).

Of the marine harpacticoids, *Longipedia coronata* Claus, *L. scotti* G. O. Sars, and *L. minor* T. A. Scott have been reared sufficiently to reveal specially significant aspects of their biology (A. G. Nicholls, 1935). *Tigriopus fulvus* (Fischer) has also been studied in considerable detail by Fraser (1936) and Shaw (1938). The morphology of the larval stages of a number of other marine harpacticoids has been described by various investigators, especially Chappuis (1916), Brian (1919, 1922), Gurney (1930, 1932), and Nicholls (1941). Many of the littoral species, though less conspicuous than planktonic copepods, fill an important niche as microscavengers on the bottom, and therefore warrant a close study for ecological reasons.

Tisbe furcata, also known under the generic names of *Idya* and *Idyae* (see Wilson, 1932), is a littoral cosmopolitan species. It thrives in cultures and therefore often occurs as a contaminant in laboratory cultures of other organisms. At Scripps Institution it is constantly present in the salt-water system, aquariums, etc., to which it gains entrance from the sea through the pumping system.

In 1934 it occurred in such numbers that it contributed materially to formation of flocculent detritus in the pipes. This detritus when matted together with loosened calcareous tubes of *Spirorbis* (also established in the system) caused serious clogging of water delivery jets in the aquariums.

There is some possibility that "culture forms," characterized by small differences in proportions of appendage segments and strength of setae, may develop in *Tisbe* in these cases of isolation or semi-isolation from the "wild" population. However,

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Monk (1941) considers the present form to be a new variety, *johnsoni.* Controlled tests were not made of the factors involved in development of culture forms, but the temperature range (about 17–21° C.) over which the animals were reared is small compared to that used by Coker (1934) in experiments affecting the form of fresh-water *Cyclops.*

In nature *Tisbe furcata* is usually found in shallow water among algae or on the bottom where it is frequently the dominant species, but being capable of swimming, it is sometimes found also in the coastal plankton. Sars (1903–1911), who has given a full description of the adult, found it to be the most widespread of the harpacticoids in Norway wherefrom he also reports a large deep-water form of the species.

The Developmental Stages

During its life cycle *Tisbe furcata* passes through six naupliar and six copepodid stages, the last of which is the adult. The female is about 1.0 mm. and male 0.7 mm. long. The instars are separated by only one molt as in other copepods that have been studied. The female carries the eggs in a single egg-sac attached to the genital segment. The early cleavage and embryological stages have been studied by Witschi (1934).

All drawings have been made from specimens reared in the culture experiments to be described later. The assistance of Dr. Cecil R. Monk is gratefully acknowledged in connection with the 1938 cultures and with the developmental stages.

Naupliar Stages

(Plate I, Figs. 1 to 6)

In all these stages the larvae are normally benthonic, but occasionally they are taken in the plankton near shore where they have been swept off the bottom by water currents. They are colorless, subcircular in outline and possess a small red eye spot.

Nauplius Stage I (Fig. 1).—Average length 0.062 mm.; labrum circular flap; first antennae three-segmented, the distal segment with three terminal setae; the second antennae strongly built, the endopod terminating in a prehensile hook, exopod normal. The first basis of the second antennae is provided with a large but rudimentary masticatory blade or hook with a small seta at its base, and the second basis bears two strong spines. The mandibular palp possesses a splender exopod of three indistinct segments, the distal segment bearing one short and one very long seta; the endopod bears two strong short hooks and two setae. The caudal armature consists of two rather long flaccid setae.

Nauplius Stage II (Fig. 2).—Average length 0.082 mm. The obvious structural advancements over Stage I consist of increase in strength of the masticatory blade of the second antennae and the appearance of two strong setae, one each on either side of the posterior ventral side. These setae are the earliest visible fundaments of the first maxillae. This early appearance of the maxillae is characteristic of the harpacticoids. In the strange nauplius larvae of *Longipedia* the first maxillae are present already in the first stage (Nicholls, 1935). In this respect the development of harpacticoids is similar to that of many cyclopoids. In calanoids the rudiments of these appendages first appear in the third or fourth nauplius stage.

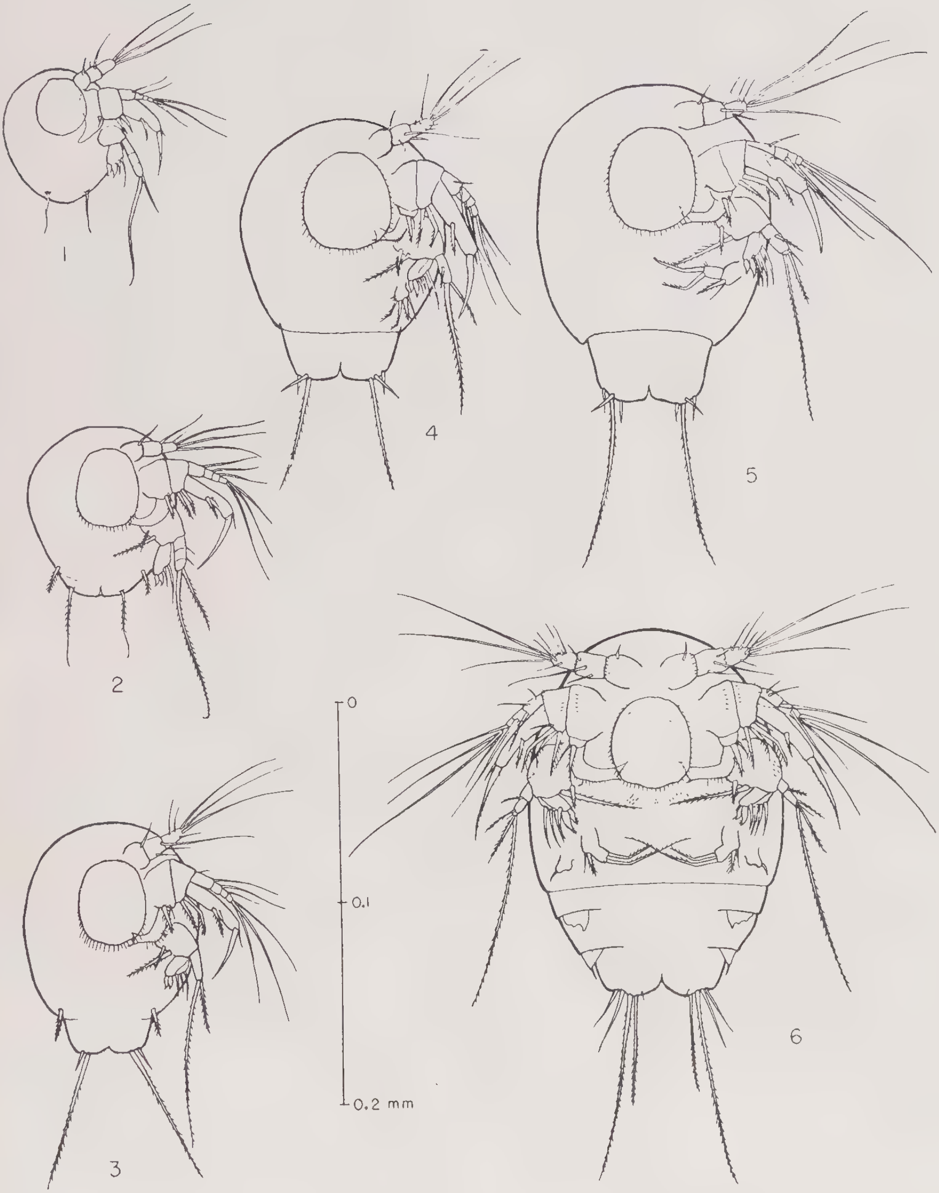

PLATE I

Development of *Tisbe furcata*

FIGURES 1–6. Nauplius stages I to VI—ventral; all drawn to same scale with aid of camera lucida.

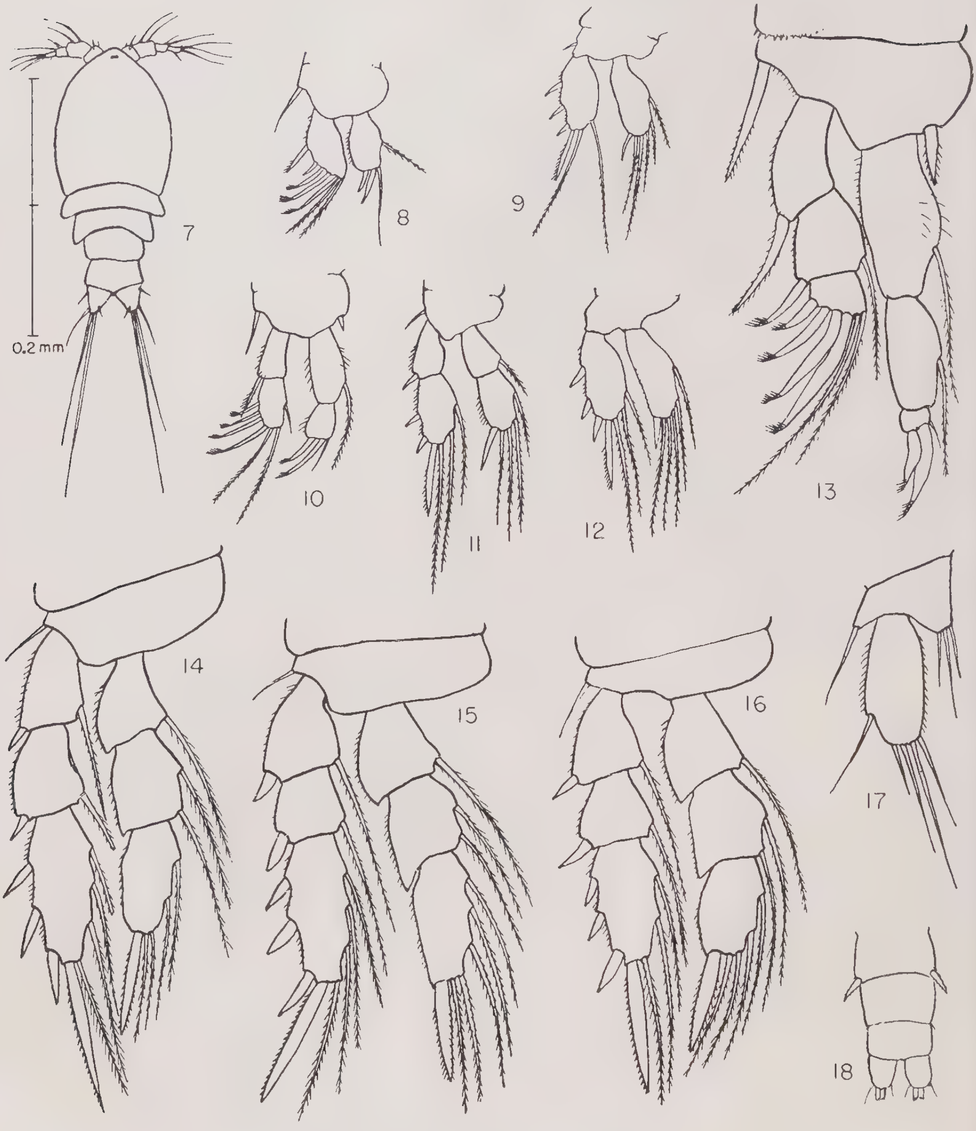

PLATE II

Development of *Tisbe furcata*

(*Camera lucida* drawings)

FIGURE 7. Copepodid stage I—dorsal.

FIGURES 8 and 9. First and second feet—Copepodid stage I.

FIGURES 10, 11, AND 12. First, second and third feet—Copepodid stage II.

FIGURES 13, 14, 15, 16, AND 17. First, second, third, fourth, and fifth feet—Copepodid stage V—female.

FIGURE 18. Posterior ventral portion of urosome of male copepodid stage IV to show sixth feet as represented by spines.

Nauplius Stage III (Fig. 3).—Average length 0.110 mm. As in II, but with three marginal setae on the distal segment of the first antennae, one additional seta on the endopod of the mandibular palp, and one short seta issuing from the outer angle of each caudal ramus. The original caudal setae are now much longer and more rigid than before.

Nauplius Stage IV (Fig. 4).—Average length 0.130 mm. As in III, but posterior segment of body more clearly defined. The distal segment of first antennae with increased number of marginal setae that can be discerned only with difficulty and are therefore not useful in identification as in calanoid larvae. The endopod of mandibular palp with four setae; the first maxillae, each showing one segment with three spines and a long seta; each caudal ramus with two short outer setae at the base of the long seta.

Nauplius Stage V (Fig. 5).—Average length 0.156 mm. As in IV, but the rudimentary first maxillae have two segments each, the distal segment with two strong curved spines and the proximal with one spine and one seta. Caudal ramus each with an additional short seta set at the inner base of the long seta making a total of three short setae.

Nauplius Stage VI (Fig. 6).—Average length 0.178 mm. As in V, but distal segment of first antenna with five marginal setae; one-segmented rudiment of second maxilla is evident with one short seta; rudiments of first and second pairs of legs present but the maxillipeds were not evident. Caudal armature as in V, but the formerly short setae are much longer, especially the inner pair.

Copepodid Stages

(Plate II, Figs. 7 to 18)

The sixth nauplius stage metamorphoses to the first of six copepodid stages, the last of which is the adult. The period required to pass from hatching of the first nauplius to the last copepodid is about 16 days at temperatures of 17° to 21° C.

The first copepodid stage is 0.20 mm. long and resembles the adult in general appearance, but there are present only the first two pairs of feet with a rudiment of the third pair and the metasome and urosome have respectively only three and two divisions, using the terminology of Sars. In subsequent stages one additional pair of feet is added for each molt except the fifth.

The order of segmentation of the feet follows the same pattern as that found in calanoid copepods. Each pair of feet at the time of its appearance possesses only one segment in each ramus, and in the next following molt each ramus becomes two-segmented and remains thus until the fifth molt (Copepodid V) when the rami of all the feet, 1 to 4, acquire three segments each (Plate II, Figs. 13–16). The new segment is derived from the proximal portion of the distal segment. This is illustrated in the first pair of feet which already in the fifth copepodid stage furnish diagnostic features of the genus. The fifth pair of feet which furnish the specific characters are not completely diagnostic until the sixth copepodid stage.

The sexes are readily separable morphologically in the fourth copepodid stage. The male in this stage is not only smaller in body size but the sixth pair of feet is already clearly developed, each foot represented by a small spine (Plate II, Fig. 18).

In the female these feet are wanting or indistinguishable from the row of fine spines on the urosome.

THE BIOLOGY OF TISBE FURCATA

Culture experiments

Syracuse watch glasses and low stender dishes of 50 ml. capacity were used for culture dishes in order to facilitate direct examination under the low-power microscope. The water used in the dishes was filtered to eliminate the possibility of contamination with foreign eggs or nauplii from the general sea-water supply. A fairly constant temperature was maintained by keeping the culture dishes on a table of running sea water, though the animals thrive in dishes kept at ordinary room temperatures.

A variety of marine foods was tested including ground dried mussels and scallops, dehydrated kelp, fresh seaweed and fecal pellets of *Nereis*. Each of these given individually in very small amounts was quite satisfactory as food. Shavings of fresh brown seaweed or dehydrated kelp appeared to be the best single food. Fresh seaweed has the disadvantage that the slime secreted tends to entrap the organisms. In general, however, the cultures were fed various mixtures of the above items so that some measure of selection was possible for the animals. About twice a week the dishes were cleaned by removing the debris and about one half of the water with a pipette, and a fresh supply of water and food added.

Life history series were obtained in four separate years, i.e., March-May 1935, June-July 1938, April-June 1942, and Sept.-Dec. 1947. During this time 30 or more broods and some of their progeny for two generations were studied more or less completely. During these periods no marked seasonal changes were observed in the breeding habits, or rate of reproduction, though a somewhat higher average number of eggs per egg-sac was noted in December.

Since observations on the 1942 series were the most continuous, they will form the main basis for discussing the salient features in the biology and life cycle of this species. Where data can be drawn from the earlier or later cultures, they will be made a part of the summary of time involved in the various phases or periods of the life cycle.

The lapse of time given for the various periods is the minimum time, or the average of several observed minima. For example, the first appearance of a nauplius in a culture was set as the beginning of the naupliar period and the first appearance of a copepodid marked the end of the naupliar period for any one brood.

Number of eggs produced

In order to obtain an estimate of the average number of eggs produced by each female per brood, counts were made of the eggs in the brood sacs of ten ovigerous females selected at random from the general population in March 1942. The number ranged from 29 to 82, with an average of 42.9 eggs per sac. There is obviously a very wide range in the number of eggs produced per egg-sac depending upon how long the individual has been laying eggs, and perhaps also upon the season. A check count was made in December 1947 in which the numbers ranged from 45 to 93 with an average of 72 eggs in each of 12 egg-sacs. Kunz (1935) reports 30 to 41 eggs for the species in Kiel Bay.

A group of ten ovigerous females was selected at random from the same population from which the 1942 egg counts were made and isolated for experimental culture, two females per dish. Each female was removed from the dish as soon as her eggs had all hatched. Thus each of the five culture dishes contained the nauplii from two egg-sacs. Careful account was kept of each population. As they matured and the adults mated, each mating pair was removed, recorded, and placed in another dish. In this way an accurate census was obtained.

Success of hatching and survival

From the ten broods 343 individual animals reached maturity. This indicates about 80 per cent survival, if we assume that the average egg-sac contains 43 eggs.

Incubation period

The duration of the incubation period was approximated by noting the first appearance of the egg-sac and the subsequent hatching of the nauplius larvae from the sac. The minima obtained ranged from two to four days. On the basis of the average of 21 cases the period was 2.5 days. Usually the cultures were examined every one to three days.

Naupliar period

The time required for completion of the separate stages was not studied. During the naupliar stages the animals creep about actively over the bottom or cling to detritus, etc., by means of prehensile hooks on the second antennae (Plate I, Figs. 1–6). The duration of this period is from three to eight days, with an average minimum of five days based on 22 brood histories.

Sex ratios

Of the 343 individuals reaching maturity 114 or only 33.3 per cent were females. One culture dish produced 34 females and 33 males, but in all of the rest the males were in great majority. In order to compare this unequal sex ratio in the culture dishes with that of the general population an examination was made of 44 adults from the water system. Of these only 41 per cent were females. Additional analysis involving 98 specimens reared in December 1947 also showed a ratio of one female to two males.

The numerical dominance of males is of considerable interest since usually in other species of copepods the females are the more numerous, sometimes overwhelmingly so. This inequality of the sexes is often seasonal, but no seasonality has come to light in the study of *Tisbe.*

In a study of the tide pool harpacticoid *Tigriopus fulvus,* Tsen-Hwang Shaw (1938) found 58.8 per cent females in a collection of 318 specimens.

Sexual maturity

A study of the rate at which sexual maturity was attained by 87 pairs of the 343 individuals hatched from the ten egg-sacs mentioned above, showed that two pairs began mating (as indicated by clasping) just 14 days after they had hatched. The last four pairs mated in 25 days. The average time required to reach mating maturity after hatching was 16 days. The minimum period observed in earlier experiments at Scripps Institution was ten days. The period of clasping varied from a few hours up to one or more days, but there was no evidence that the actual transfer of the spermatophore to the female is delayed until she molts to the last or sixth copepodid stage. Clasping was rarely observed before the female had reached the sixth copepodid stage, and on only one occasion was there evidence of molting during the clasping period. This point deserves further study. Williams (1907) found that for the harpacticoids, *Harpacticus uniremis, H. gracilis,* and *Tachidus littoralis,* "every successful copulation must be prolonged until the female molts."

Length of generation

The lapse of time between the hatching of one generation and the first appearance (hatching) of the next generation resulting from the above matings varied from 17 to 24 days at temperatures of 17° to 18° C. during the spring months. The maximum period observed in one case was 31 days. In 1935, two individuals required 20 days and one individual only 16 days. MacGinitie (1937) in an incidental statement records that this species completes its life cycle in ten days at Corona del Mar, California.

The time required for *Tisbe* to develop from egg to production of eggs is comparable to that reported for various species of the freshwater cyclopoid *Cyclops.* Ewers (1936), for example, found that for 12 species under observation the time varied from 8 to 50 days.

It appears that *Tisbe furcata* may complete its life cycle in about one-half the time required for *Tigriopus fulvus* which under favorable conditions in the laboratory at University College of Hull required about two months (Fraser, 1936). However Tsen-Hwang Shaw (1938) states that for this species at Pacific Grove, California, the adult stage is reached in about one month. It is probable that the Pacific Grove species is distinct from *T. fulvus,* since Monk (1941) mentions only *T. californicus* from the coast.

Number of broods produced

In order to determine the approximate number of broods produced by a single female, four of the above 87 pairs in copula were isolated in individual dishes. Several additional males were added to each dish to afford ample opportunity for additional matings, and the males were replaced from time to time with younger mature males. (Lowndes, 1933, and Fraser, 1936, infer that the presence of males stimulates egg production.) Nauplii were removed from the dishes as soon as they appeared. Records were kept of the number of egg-sacs produced by each female under these conditions. One female produced 12 broods between May 9 and June 10. Two other females each produced nine broods in the same period and one produced five broods in 20 days before dying, apparently prematurely. The first egg-sacs produced were the largest, and the last two or three produced were about half the size of the first. The egg-sacs appeared with regularity, two to five days elapsing between hatchings with three days as the average period.

Although males were kept in the presence of the females during the whole period, only one mating was observed to take place and this preceded the entire period of egg laying. In order to test further this observation in a more crowded condition as often occurs in nature, four separate cultures were set up each containing from 8 to 20 pairs of newly matured adults in copula. A total of 54 pairs were involved. All pairs in any one dish were from the same brood and therefore of the same age. At two day intervals all adults were transferred to fresh culture dishes so that their generation could be kept separate from the younger generation constantly being produced. These adults were maintained from May 12 to June 12, and during the time following the separation of the pairs originally mated, only one instance of a second clasping was observed. This instance occurred 21 days after the original mating, and it is not known if a spermatophore was transferred. The pair concerned was isolated from the rest of the culture in order to determine if the female would continue to produce eggs for a longer time than the other females as a result of this second mating. However, no additional eggs were carried by her. This is in agreement with the earlier observations where in one case a succession of seven broods was produced by a female that had been reared in culture and isolated following one mating. She lived 70 or 71 days but produced no eggs after the 53rd day. In another test 11 ovigerous females isolated from the general population produced two to five broods, but it is not known if previous broods had been produced before isolation. Nicholls (1935) has reported a case in which a female specimen of *Longipedia scotti* had produced at least nine broods during a period of isolation from contacts with males.

The question naturally arises as to whether or not the male of *Tisbe* produces a succession of spermatophores and remains fertile after the first mating. To test this, a single male was isolated from a group of newly matured virgin males. Several virgin females were added to the dish at intervals, and records were kept of the fertility of eggs subsequently produced by each female. Out of a total of 13 virgin females brought into contact with this one male, six produced fertile eggs which hatched. The other seven females produced eggs which failed to hatch. In another test one male fertilized eight females which produced fertile eggs.

Virgin females kept in isolation have produced full egg-sacs, but in no instance was there any evidence of parthenogenesis as reported by Roy (1931) for the harpacticoid *Canthocamptus bidens*. Pine (1934) has reported parthenogenetic reproduction in *Cyclops viridis*. This, however, appears to be a misinterpretation resulting from failure to note that several egg-sacs with fertile eggs may be produced following only one mating. The females with which she worked were doubtless already fertile since they were isolated in the gravid condition from the wild.

Discussion

Rather little is known regarding the kinds of predators that feed directly upon the littoral copepods. That this type of animal food constitutes an appreciable source of nourishment for littoral animals is suggested by the fact that only a moderate population of *Tisbe* has been observed in the sea despite a relatively rapid and steady rate of replenishment as suggested by the present study. Being detritus feeders with a wide range of acceptable food, it is probable that in favorable habitats *Tisbe* population density is controlled largely by predators. Among these predators are no doubt small fish capable of capturing small prey of this kind by pursuing and picking up the copepodid stages individually, and coelenterates having tentacles supplied with nematocysts and viscid surfaces that enable capture by chance contact. Various detritus feeders scooping up particles of detritus would consume together with this many *Tisbe,* especially the nauplii, that are prone to cling to particles upon which they are feeding.

From the present study it appears that an average of about 513 eggs is produced by each female in her lifetime. This is calculated from an average of 57 eggs per brood (using the averages of March and December) and a total of nine broods. For unknown reasons only about 80 per cent of the larvae hatched in the cultures survived to adult state. Thus, using the above figure for one female, 410 survive, of which only about 135 (approximately one third) are females. Considering a succession of generations each 25 days, a prodigious number of progeny is possible, for in about 100 days (fourth generation) over 1 billion 55 million individuals of both sexes would be produced. Ten males plus 5 females make up a mass of about 1 $mm.^3$. Hence in 100 days 70 liters of copepods would have been produced.

TABLE I

Potential rate of reproduction in Tisbe furcata and Calanus finmarchicus in cultures

	No. of broods or spawnings	No. of eggs per brood or spawning	Total no. of eggs in life-time of one ♀	Interval between generations	Survival to adult
Tisbe	7–12 average 9	29–93 average 57	513	15–31 days usually 19–24 days	80%
Calanus	1–3 (4?)	1–120 usually 15–70	Maximum observed 120	Minimum 41 days	?

These figures can of course have no significance other than to emphasize that the animal substance which *Tisbe* could supply is considerable and that a very large number of copepods must be consumed regularly by enemy predators in order to keep a balance between consumption and reproduction.

It is instructive to compare certain vital aspects of the life history of this important littoral species with similar aspects of *Calanus finmarchicus,* the most widely studied of planktonic-copepod species.

In view of the vast swarms of *Calanus* which sometimes occur in the sea, one might expect that studies of its rate of reproduction would reveal aspects suggesting possibilities of greater individual fecundity than occurs in *Tisbe,* a seemingly less abundant species. In no instance, however, is a greater rate of reproduction shown for *Calanus* on the basis of studies that have thus far been made in cultures.

Table I compiled mainly from Nicholls (1933), Clarke and Zinn (1937) and Raymont and Gross (1942) shows the great discrepancies that are brought out when comparing these two genera of widely different ecological habits.

The life span of *Calanus* is greater than that of *Tisbe,* but this appears to have no bearing on the fecundity since the number of spawnings is not shown to be affected thereby. Raymont and Gross found that under laboratory conditions *Calanus* was capable of spawning throughout the year, similar to our observations for *Tisbe,* but field observations by numerous investigators show that the rate of reproduction for *Calanus* in the sea varies greatly with season, there being a marked minimum in autumn and winter when the animals survive in copepodid Stage V. No similar field data are available for *Tisbe.*

The usually great preponderance of females over males in *Calanus* should enhance the reproductive rate provided this preponderance obtains also for the hatching eggs and provided further that there are always sufficient males in the population. That the latter is probably true is indicated by the study of Gibbons (1933). There is some evidence that in *Calanus,* as in *Tisbe,* one mating may suffice for continued spawning, since females have been observed to produce fertile eggs three or four weeks after isolation.

The greater ratio of males to females in *Tisbe* seems to have no logical explanation, since it is shown that one mating suffices for all the broods the female can produce, and each male produces a sufficient number of spermatophores to fertilize seven or eight females.

In considering this anomalous situation with respect to the relative reproductive rate of the two genera in cultures contrasted with their abundance in nature, the answer might be found in the greater ease with which *Tisbe* can be reared in culture. Hence, a truer picture might be obtained for that genus, but one that is difficult to check in the field. It is probable that in nature *Calanus* actually reaches reproductive maturity at a younger age and produces more eggs than have thus far been shown in culture experiments or deduced from field observations. An obvious alternative is that the survival rate is greater for *Calanus* (possibly because of greater opportunity for dispersal both vertically and laterally). The conclusion must then be that *Tisbe* is heavily preyed upon in its natural habitat.

SUMMARY

1. *Tisbe furcata* is a littoral copepod that commonly invades salt-water systems connected with the sea. It is readily reared through all of its developmental stages. Being a scavenger, it thrives on various types of food, but thin slices of fresh seaweed and dehydrated kelp were especially acceptable.

2. Following the egg, there are six naupliar and six copepodid stages, the last of which is the adult. Each stage is separated by one molt.

3. The incubation period is from two to four days, usually about 2.5 days.

4. The total duration of the naupliar stage is three to eight days, usually about five days.

5. The first indication of sexual maturity as shown by clasping by the male occurred between the 10th and 25th days, usually about the 16th day.

6. The minimum time between generations (i.e., from egg to egg production) was 15 days, but usually between 19 to 24 days.

7. The span of life of individuals varied greatly. It was studied mainly in the females, some individuals of which lived for 40 to 50 days. The oldest specimen had a life span of 70 or 71 days, but no eggs were produced after the 53rd day.

8. The number of broods indicated by egg-sacs produced by isolated females varied from 7 to 12, with an average of about 9. Following the first egg sac, the subsequent ones appeared at intervals of two to five days, usually about three days.

9. The number of eggs in a brood varied from 29 to 93 with an average of 43 in one sampling and 72 in another.

10. Each female mated but once, and this mating sufficed for fertilization of all of the eggs to be produced. Males were capable of several matings.

11. About 80 per cent of the larvae hatched survived to adult state.

12. There is no evidence of parthenogenesis.

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Contribution No. 400

SOME EMPIRICAL RELATIONS BETWEEN SEASONAL[1] VALUES OF $(E-P)$ AND SURFACE SALINITIES OVER THE NORTH ATLANTIC[1]

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In the absence of horizontal flow, the surface salinity of any part of the ocean is mainly determined by three processes: Decrease of salinity by precipitation P, increase of salinity by evaporation E, and change of salinity by vertical mixing. Where $(E-P)$ is a positive quantity, the effect on the vertical distribution of salinity is as if salt were being diffused into the volume through the sea surface and, when $(E-P)$ is a negative quantity, the effect is as if salt were being diffused outward through the sea surface. In general, it is to be expected that regions of large $(E-P)$ will be regions of high surface salinities and regions of small or negative $(E-P)$ will be regions of low salinities. Therefore, where the horizontal transport term is small, a quantitative relationship between $(E-P)$ and surface salinity might be expected.

Wüst (1936) has found that the average annual surface salinities can be related to the average annual latitudinal values of $(E-P)$ quite accurately by a simple empirical expression of the form:

$$S_o = K(E-P) + S_k, \tag{1}$$

where S_o is surface salinity, K is a constant, S_k is a constant salinity and $(E-P)$ is given in cm/year. He finds it necessary, however, to assign different values for K and S_k for different oceans. His formulae do not apply near the coasts where the horizontal transport term tends to be large and where the effects of runoff from land surfaces may be important. They also do not apply near the Equator.

On the basis of previously derived seasonal evaporation and precipitation data for the oceans (Jacobs, 1948), it has been possible to obtain seasonal $(E-P)$ values for the North Atlantic and North Pacific. It is considered of interest to determine whether or not a simple empirical relation can be found between the seasonal salinities and the seasonal quantities of $(E-P)$, similar to the relations found by Wüst, when we consider mean annual values. Unfortunately, seasonal salinity data are not available for the Pacific, while $(E-P)$ values are not available

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for the South Atlantic because computations of evaporation have not been possible for the latter region. Since the region must be one within which the transport of surface waters is at a minimum, the choice of areas left for analysis is limited.

An examination of current charts for the oceans (U. S. Hydrographic Office, 1945) indicates that the only completely suitable area is the one in the North Atlantic bounded by the 20th and 30th parallels and the 60° W and 20° W meridians. This section excludes the coastal areas with their pronounced N – S surface currents and is yet of sufficiently large lateral extent to minimize the effects of E – W flow.[2]

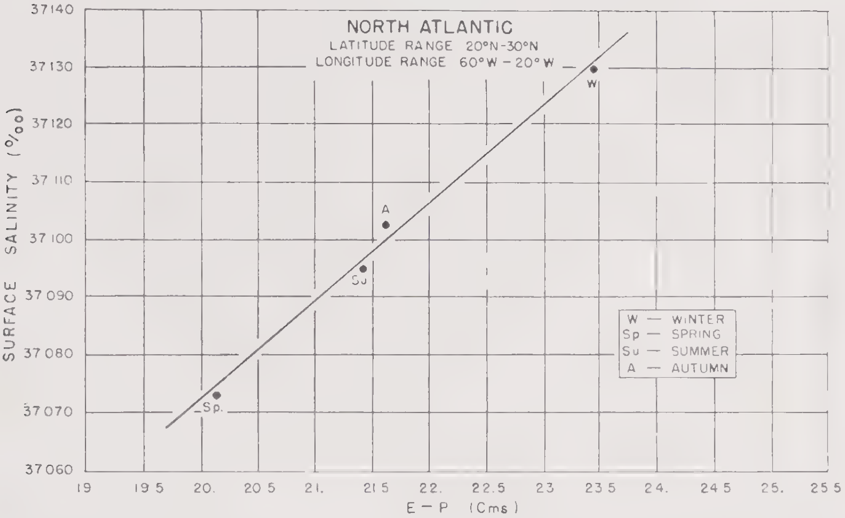

Figure 1. Surface salinity as a function of seasonal ($E-P$) in an area of the North Atlantic where the transport of surface waters is at a minimum (Lat. 20°–30°N; Long. 60°–20° W).

The results of plotting the seasonal salinity values against the seasonal ($E-P$) values for this area are given in Fig 1. An almost perfect straight line relationship is shown such that the surface salinities can be given very accurately by the formula:

$$S_o = 0.0171\ (E - P) + 36.730 \pm 0.003\ (\text{‰}). \qquad (2)$$

The range of salinities computed through its use differs from the observed range of salinities by less than 10%.

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[2] The seasonal salinity values have been scaled from charts given by Böhnecke (1936).

Having obtained good results in the one area of the North Atlantic where the transport of surface waters is at a minimum such that the effect of advection on the surface salinity would be small, it was decided to test at least one other area even though a considerable advective effect might be expected. The area chosen for this examination is the one immediately to the north of the previous area, *i. e.*, the area bounded by the 30th and 40th parallels and by the 20th and 60th meridians.

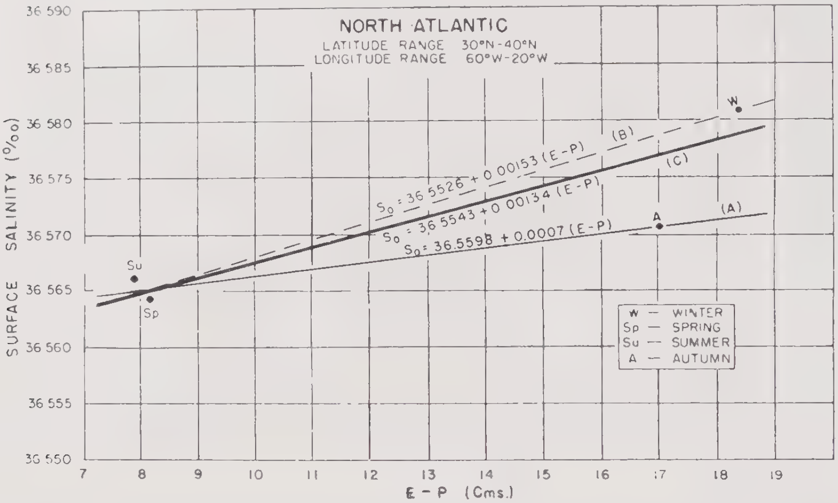


Figure 2. Surface salinity as a function of seasonal $(E-P)$ in an area of the North Atlantic where the horizontal transport of surface waters cannot be neglected (Lat. 30°–40° N; Long. 60°–20° W).

The results of plotting the seasonal values of $(E - P)$ against the seasonal salinities for this area are given in Fig. 2. Unfortunately, the seasonal $(E - P)$ values and seasonal salinities for spring and summer are so nearly identical that, for practical purposes, they both constitute a single point. The winter and autumn points, on the other hand, are so widely dispersed that no reasonable curve can be drawn that would serve to connect all points. However, as first steps in analysis, it is possible to assume that the summer, spring and autumn values are correct and that high salinity water is being advected into the area during winter (curve *A* in Fig. 2) or that the summer, spring and winter values are correct and that low salinity water is being advected into the area during autumn (curve *B* in Fig. 2).

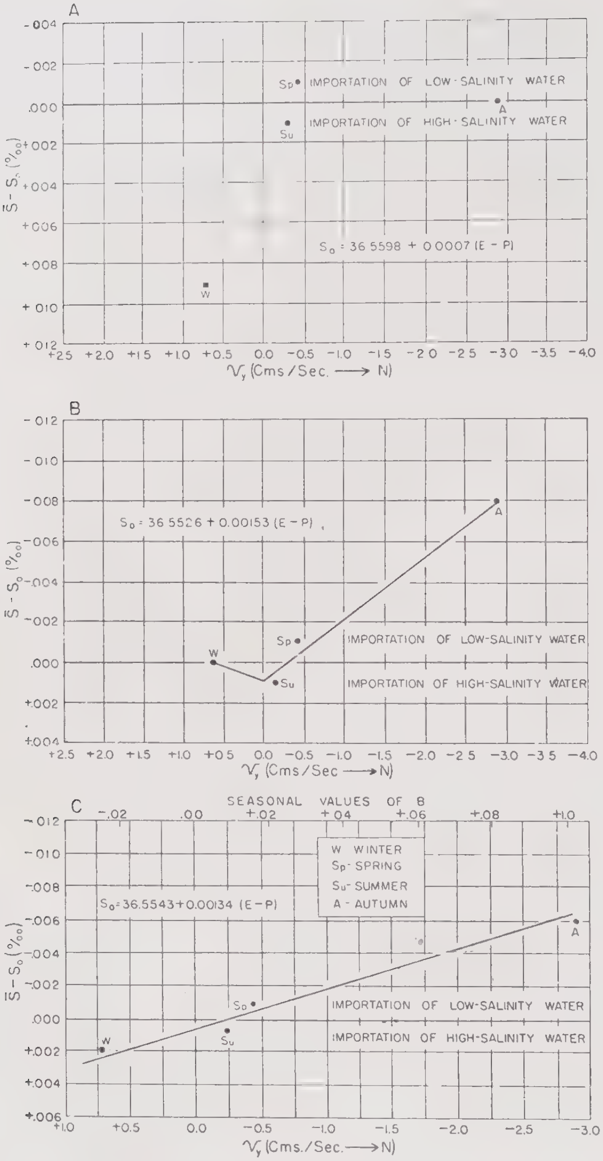
An examination of the salinity distribution over this portion of the North Atlantic, as given by Böhnecke (1936), reveals that the horizontal salinity gradients are slight except along the 40th parallel between the meridians 40° W and 60° W where very low salinity water exists. In order to determine the nature of the surface flow in this area of marked salinity gradients, monthly charts of the surface currents prepared for one-degree squares by the U. S. Hydrographic Office (1945) have been examined and the surface transport across the 40th parallel determined. The midmonths of each of the seasons were accepted as representing the average seasonal flow, and the average northerly component of flow for the area between the 39th and 41st parallels and the 40° W and 60° W meridians was computed for each of these months. The results are as follows:

Season	V_y
Winter	$+0.73$ cm sec
Spring	-0.43 cm/sec
Summer	-0.26 cm/sec
Autumn	-2.89 cm/sec,

where V_y is the component of flow across the 40th parallel, negative values indicating southerly flow (importation of low salinity water) and positive values indicating northerly flow (transport outward of waters across the 40th parallel) in accordance with usual notational practice.

Given in Fig. 3A are the results of plotting the seasonal values of V_y against the difference between the observed surface salinities, S, and the salinities computed on the assumption that the summer, spring and autumn values are correct (curve A in Fig. 2). An almost complete scattering of points occurs, indicating that the difference between the winter and autumn salinities cannot be accounted for by the advection of high salinity water during the winter season.

In Fig. 3B are plotted the differences between the observed surface salinities and the salinities computed on the assumption that the summer, spring and winter values are correct (curve B in Fig. 2) against the seasonal values of V_y. The three points representing the summer, spring and autumn months fall nicely along a straight line, but the winter value proves to be about 0.003 °/₀₀ too high to be accounted for merely by an absence of advection of low salinity water. However, since the winter season is the only one which shows positive values for V_y (transport toward the north across the 40th parallel), it is reasonable to construct the curve as shown in Fig. 3B by simply connecting the points by two straight lines which intersect at a common point


A
- 004
- 002
.000
+ 002
+ 004
+ 006
+ 008
+ 010
+ 012
$\bar{S} - S_o$ (‰)
Sp
A
Su
W
IMPORTATION OF LOW-SALINITY WATER
IMPORTATION OF HIGH-SALINITY WATER
$S_o = 36.5598 + 0.0007 (E - P)$
+2.5 +2.0 +1.5 +1.0 +0.5 0.0 −0.5 −1.0 −1.5 −2.0 −2.5 −3.0 −3.5 −4.0
V_y (Cms/Sec. ⟶ N)
B
- 012
- 010
- 008
- 006
- 004
- 002
.000
+.002
+.004
$\bar{S} - S_o$ (‰)
$S_o = 36.5526 + 0.00153 (E - P)$
A
Sp
W
Su
IMPORTATION OF LOW-SALINITY WATER
IMPORTATION OF HIGH-SALINITY WATER
+2.5 +2.0 +1.5 +1.0 +0.5 0.0 −0.5 −1.0 −1.5 −2.0 −2.5 −3.0 −3.5 −4.0
V_y (Cms/Sec ⟶ N)
C
SEASONAL VALUES OF B
−.02 .00 +.02 +.04 +.06 +.08 +1.0
- 012
- 010
-.008
-.006
-.004
-.002
.000
+.002
+.004
+.006
$\bar{S} - S_o$ (‰)
W WINTER
Sp - SPRING
Su - SUMMER
A - AUTUMN
$S_o = 36.5543 + 0.00134 (E - P)$
A
Sp
W
Su
IMPORTATION OF LOW-SALINITY WATER
IMPORTATION OF HIGH-SALINITY WATER
+1.0 +0.5 0.0 −0.5 −1.0 −1.5 −2.0 −2.5 −3.0
V_y (Cms./Sec. ⟶ N)

(Figure 3)

along the line where $V_y = 0$ and to make no assumptions regarding the nature of the surface transport of salinity during the winter season.

However, since there is northerly transport of surface waters across the 40th parallel only during the winter season, and considering the fact that, except along the 40th parallel, the salinities of surrounding areas tend to be slightly higher than within the region under consideration, it is more reasonable to assume that water of higher salinity is being advected into the region during winter, the amount advected being proportional also to V_y. On the basis of this assumption the curve C in Fig. 2 has been constructed. As shown by Fig. 3C, V_y plotted against the differences between the observed seasonal salinities and the salinities computed on the basis of curve C indicate an almost perfect straight-line relationship.

Curve C in Fig. 2 can be represented by the following formula:

$$S_o = 0.00134\,(E - P) + 36.5543 \qquad (°/_{oo}), \tag{3}$$

while the curve in Fig. 3C can be represented by the expressions:

$$\bar{S} - S_o = 0.00246 V_y + 0.00071 \qquad (°/_{oo}) \tag{4}$$

or

$$V_y = 406.25(\bar{S} - S_o) - 0.2875 \qquad (\text{cm/sec}). \tag{5}$$

Combining expressions (3) and (4), a simple empirical formula is obtained which allows the surface salinity to be computed with exceptional accuracy. In this case,

$$S_o = 0.00134(E - P) + 0.00246 V_y + 36.555 \pm 0.001 \ (°/_{oo}), \tag{6}$$

where V_y is in cm/sec.

Because of the paucity of subsurface current and salinity data in these regions and because of the complicated nature of the vertical and lateral mixing processes which are involved, it does not appear profitable at this time to attempt to determine, on the basis of theoretical considerations, the significance of the salinity and $(E - P)$ relationships which have been illustrated.

Figure 3. Difference between the computed (S_o) and observed ($\bar{S}$) salinities for the area in the North Atlantic Lat. 30° to 40° N and Long. 60° to 20° W as a function of the transport of surface waters across the 40th parallel between the meridians 60° W and 40° W.

A. The relationship with the northerly component of surface flow, V_y, assuming the relation between $\bar{S}$ and $(E-P)$ as given by curve (A) in Fig 2.

B. The relationship with V_y, assuming the relation between $\bar{S}$ and $(E - P)$ as given by curve (B) in Fig. 2.

C. The relationship with V_y, assuming the relation between $\bar{S}$ and $(E - P)$ as given by curve (C) in Fig. 2.

The values for the ratio, b, between volume of water advected and total volume of water within the mixing layer (assuming V_y constant with depth throughout the mixing layer) are entered along the top margin of graph.

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